Biodiversity and Ecosystem Functioning across Scales in Real-World Landscapes

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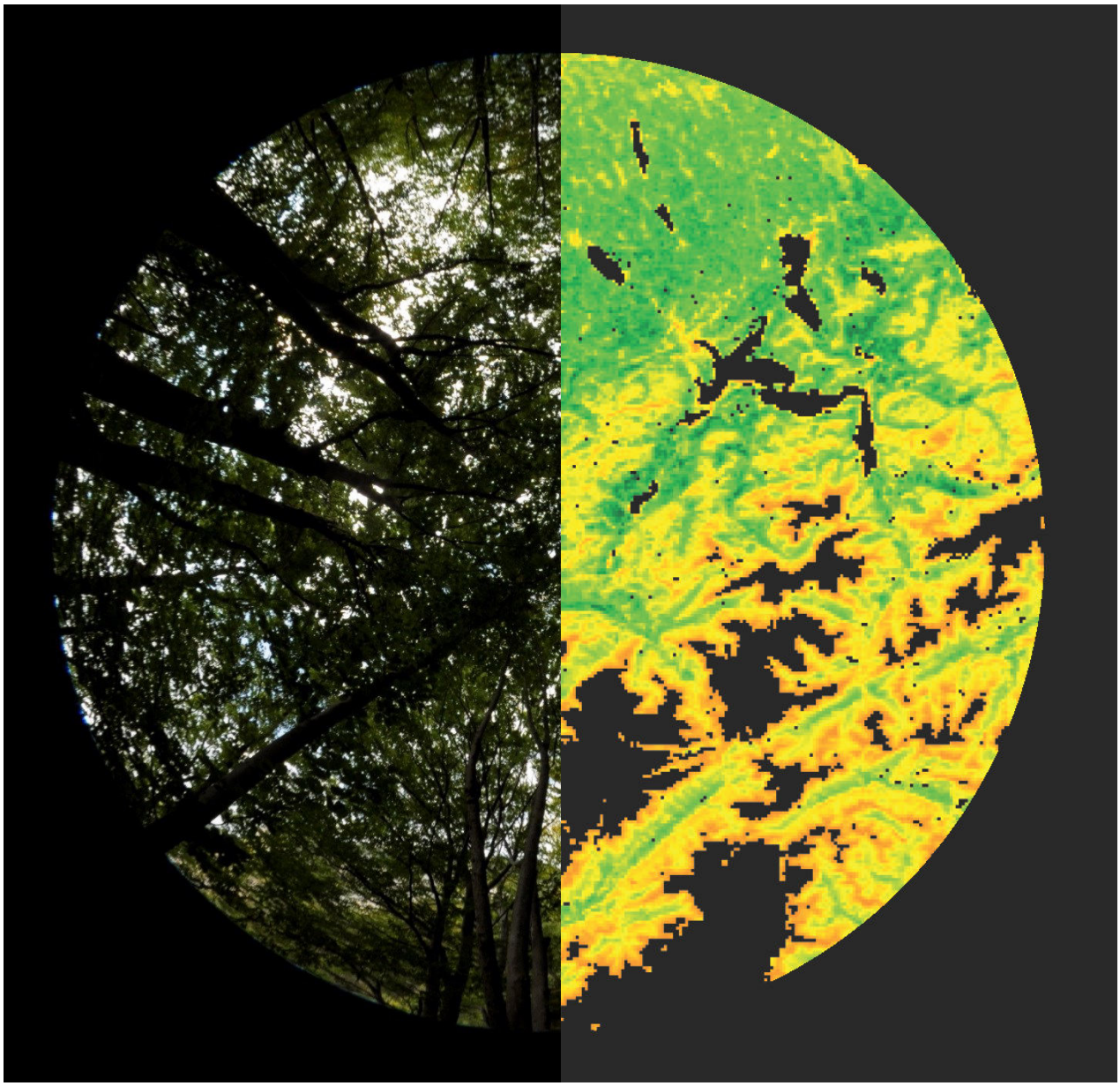
I dedicate this thesis to my father Fredi Oehri, who gave me the gift to marvel at the stunning beauty that surrounds us in the most obvious and most hidden places. What a fascinating circumstance that things exist, somehow, and what a wonderful chance to be here and contemplate.



Forest canopy in a photographer's perspective (left), primary productivity in a satellite's perspective (right).

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Summary

Biodiversity, the variability of life on all levels from genes to ecosystems, is currently declining globally due to human activities. Research has shown that biodiversity is a fundamental promoter of ecosystem functions that support human existence. This reveals the potentially devastating consequences of biodiversity loss for human well-being. However, most biodiversity-ecosystem functioning (B-EF) research was conducted in simplified, experimental settings at small spatial scales, and knowledge on the consequences of biodiversity loss in complex natural or managed landscapes of the "real world" is still very limited.

In my thesis, I elucidated the relevance of biodiversity for ecosystem functions at large scales of space, time and ecological organization in real-world landscapes across Switzerland.

In chapter 1, I comparatively analyzed effects of tree species and land-cover type diversity on local forest functions and determined their interrelation with environmental context at the local and landscape scale. I found that local tree diversity is an important determinant of forest productivity and growing season length, whereas landscape diversity likely only indirectly influences these ecosystem functions via positive effects on tree diversity. Tree diversity effects were relatively consistent across the large environmental gradients covered by the study.

In chapter 2, I studied the effects of ecosystem diversity approximated by land-cover type richness on the satellite-sensed functioning and stability of landscapes with an area of 62'500 and 250'000 m^2, respectively. I selected these landscapes using geographic information data according to an orthogonal and balanced study design. I found that landscape-level productivity, growing season length and the inter-annual stability of these variables increased with land-cover type richness in the time of 2000-2016. Also the inter-annual stability of near-infrared surface albedo increased with land-cover type richness. These land-cover type richness effects were consistently higher in landscapes of larger spatial extent.

In chapter 3, I investigated effects of regional species diversity on satellite-sensed ecosystem functioning in 1 km^2 – landscapes. I found that regional species diversity of plants, birds and butterflies is strongly related to increased vegetation productivity, increased inter-annual stability of productivity, and to an accelerated lengthening of the

growing season in the time of 2000-2015. Species diversity effects were independent of environmental context such as altitude and relatively large compared to effects of topography, climate and land cover.

Overall, I found empirical evidence supporting the view that biodiversity is of great importance for ecosystem functioning and stability in complex real-world landscapes. The biodiversity effects I found were consistent across environmental gradients and relatively strong compared to effects of other important environmental drivers. Also, these effects were similar or even larger in size than the effects found under experimental conditions. Intriguingly, I found positive diversity effects not only for local and landscape-level species diversity (α- and γ- diversity, respectively), but also for the spatial diversity of ecosystem types (i.e. β-diversity). Finally, I found diversity effects on ecosystem functions beyond primary productivity's temporal average and stability. I found diversity effects on vegetation phenology and the temporal stability of land surface albedo, which contribute to the adaptive capacity and the climatic stability in complex real-world landscapes.

Hence, my findings highlight the generality and the importance of diversity effects across large scales of space, ecological organization and various hitherto underexplored ecosystem functions important for landscape resilience.

Zusammenfassung

Biodiversität, die Vielfalt der Lebensformen auf allen Ebenen, von Genen bis zu Ökosystemen, verschwindet weltweit aufgrund von menschlichen Aktivitäten. Die Forschung hat gezeigt, dass Biodiversität essentiell für das Funktionieren von Ökosystemen ist, von welchem die menschliche Existenz abhängt. Der grösste Teil der Forschung, welche sich mit den Auswirkungen von Biodiversität auf sogenannte Ökosystem-Funktionen beschäftigte, hat dies bis jetzt mit einem Fokus auf Experimente in kleinen Versuchsflächen getan. Das Wissen um die Rolle der Biodiversität für Ökosysteme in natürlichen oder bewirtschafteten Landschaften der „tatsächlichen" Welt ist jedoch immer noch stark limitiert.

Aus diesem Grund habe ich in der vorliegenden Dissertation die Relevanz der Biodiversität für das Funktionieren von Ökosystemen unter realistischen Bedingungen in Schweizer Landschaften untersucht, welche sich über grosse Gradienten verschiedenster Umweltbedingungen erstrecken.

In Kapitel 1 habe ich untersucht, wie die Wald-Funktionen von der Baumartenvielfalt und von der Vielfalt der Ökosysteme in der umliegenden Landschaft beeinflusst werden. Ausserdem habe ich untersucht, wie Effekte von Baumarten- und Ökosystem-Vielfalt mit verschiedenen Umweltbedingungen zusammenhängen. Die Resultate meiner Studie zeigen, dass Baumartenvielfalt die Produktivität und die Länge der jährlichen Wachstumsperiode in den untersuchten Wäldern erhöht, und dies unter verschiedensten klimatischen und topographischen Bedingungen. Die Vielfalt von Ökosystem in der umliegenden Landschaft stand nicht im direktem Zusammenhang mit den untersuchten Wald-Funktionen. Jedoch gab es einen positiven Zusammenhang zwischen Ökosystem-Vielfalt und Baumartenvielfalt. Deshalb könnte die Ökosystem-Vielfalt die lokalen Wald-Funktionen indirekt beeinflussen.

In Kapitel 2 habe ich die Auswirkungen von Ökosystem-Vielfalt auf Ökosystem-Funktionen untersucht, welche ich von Sattellitendaten für jeweils ganze Landschaften mit 62‘500 und 250‘000 m^2 Fläche abgeleitet habe. Die Ökosystem-Vielfalt habe ich durch die Anzahl Bodenbedeckungs-typen approximiert, welche ich von Geographischen Informations - Daten abgeleitet habe. Die Untersuchungsflächen habe ich nach einem systematischen Studien-Design ausgewählt, so dass eine unverzerrte Evaluation in

unterschiedlichen klimatischen und topographischen Umweltkontexten möglich war. Die Studie hat ergeben, dass sich Ökosystem-Vielfalt positiv auf die Produktivität und die durchschnittliche Wachstumsperiode der Vegetation, sowie deren Stabilität über die Jahre 2000-2016 auswirkt. Die Ökosystem-Vielfalt hat sich ausserdem auch positiv auf den durschschnittlichen Infrarot - Albedo und dessen zeitlichen Stabilität ausgewirkt. Die Effekte der Ökosystem-Vielfalt waren zudem höher in den grösseren Landschaften (250‘000 m^2) als in den kleineren Landschaften (62‘500 m^2).

In Kapitel 3 habe ich die Effekte der regionalen Artenvielfalt auf Ökosystem-Funktionen untersucht, welche ich von Sattellitendaten für Landschaften mit 1 km^2 Fläche abgeleitet habe. Die Studie hat ergeben, dass die regionale Artenvielfalt von Pflanzen, Vögeln und Schmetterlingen stark positiv mit der Produktivität der Vegetation sowie deren Stabilität und einer verstärkten Verlängerung der jährlichen Wachstumsperiode in der Zeit von 2000-2015 zusammenhängt. Diese Biodiversitäts-Effekte waren gleich stark in verschiedenen Umweltbedingungen und oft übertrafen sie jene von anderen wichtigen Umweltfaktoren.

Zusammenfassend liefert diese Dissertation empirische Evidenz, welche die wichtige Rolle der Biodiversität für das Funktionieren von Ökosystemen in realistischen Bedingungen und auf grossen Landschaftsflächen demonstriert. Die Biodiversitäts-Effekte in meinen Studien waren konsistent über verschiedenste klimatische und topographische Umweltbedingungen hinweg. Die Biodiversitäts-Effekte waren vergleichbar oder grösser als Effekte von anderen wichtigen Umweltfaktoren und als Biodiversitätseffekte, welche in Experimenten identifiziert wurden. Interessanterweise wirkten sich nicht nur lokale und regionale Artenvielfalt (sogenannte α- und γ- Diversität) sondern auch die Ökosystem-Vielfalt (sogenannte β-Diversität) auf die untersuchten Landschafts-Funktionen aus. Diese Landschafts-Funktionen betrafen ausserdem nicht nur den grossflächigen Durchschnitt und die Stabilität der Biomasse-Produktion, sondern auch die Vegetations-Phänologie und den Oberflächen-Albedo, welche die Resilienz von Landschaften beeinflussen können.

Somit heben die Ergebnisse dieser Dissertation die Allgemeingültigkeit und die Wichtigkeit von Biodiversität für das Funktionieren von Ökosystemen hervor, eine Allgemeingültigkeit die sich über grosse räumliche und zeitliche Skalen erstreckt, sowie über verschiedenste Umweltbedingungen.

General Introduction

Definitions

Biodiversity signifies the variety of life in all its forms, functions, and levels of organization, including genetic diversity, species diversity, community diversity, and ecosystem diversity. The term stands shorthand for biological diversity and was coined by the American scientist Walter G. Rosen in the “National Forum on BioDiversity” in September 1986 (Pfisterer et al. 2005).

Ecosystems are structures and processes formed by assemblages of organisms transforming and transporting energy and matter among themselves and their abiotic surrounding (Tansley 1935; Chapin et al. 2002). Ecosystems generate functions, goods and services, such as food, fiber, shelter, the control of flood and erosion, crop pollination, and water purification, which are essential for human well-being (Myers & Reichert 1997; de Groot et al. 2002; Foley et al. 2005).

Ecosystem goods and services are defined as the direct and indirect benefits humans obtain from ecosystems, and therefore represent specific ecosystem structures or processes valued in terms of their usefulness for humans.

Ecosystem functions are processes that facilitate the provision of these ecosystem goods and services (Costanza et al. 1997; de Groot et al. 2002; MA 2005; Cardinale et al. 2012). Ecosystem functions are often grouped into four primary categories: i) regulation functions, e.g. biogeochemical cycling facilitating clean air and water, ii) habitat functions, e.g. refuges facilitating the growth and reproduction of valued plants and animals, iii) production functions, e.g. photosynthesis facilitating the provision of food and fiber and vi) information functions, e.g. organic structures facilitating spiritual development and recreation of humans (de Groot et al. 2002).

Historical overview

In the subsequent sections, I provide a historical overview of the research on biodiversity and ecosystem functioning. I thereby largely focus on biodiversity of plants and animals at high levels of organization, i.e. from species to ecosystems.

Biodiversity: a marvellous paradox

Since the emergence of a common ancestor 3-3.8 billion years ago, new species formed and disappeared on Earth in perpetual speciation and extinction events. The number of species generally increased with time, especially since the 'Cambrian Explosion' when most major animal phyla appeared in the fossil record around 540 million years ago. Hence, life is assumed to be more diverse than ever before in the history of Earth (Dirzo & Raven 2003; Benton & Emerson 2007; Wiens 2011; Cornell 2013). It is assumed that a total of 5 to 10 billion species have ever existed (McKinney 1997). Estimates of contemporary species numbers range between 5 and 11 million for terrestrial and aquatic animals and >450,000 for land plants (Pimm et al. 2014). For land plants, it is assumed that 80-90% of the species are described (Joppa et al. 2010; Pimm et al. 2014), whereas for terrestrial and aquatic animals only 14% and 9% of the species, respectively, are described (Mora et al. 2011).

The immense diversity of life forms was placed into an ecological[1] perspective by Humboldt, Darwin and Wallace (Humboldt & Bonpland 1814; Humboldt 1851; Darwin & Wallace 1858; Darwin 1859). These naturalists proposed a ground breaking, new conceptualization of nature as an entangled network of organisms interacting among each other and with their environment (cf. 'beasts and birds in forest thickets' in Humboldt & Bonpland 1814 and 'entangled bank' in Darwin 1859). In this perspective, different life forms can be limited or promoted by physical environmental conditions and are ultimately determined by speciation and extinction in the 'struggle for existence' (Darwin 1859).

[1]Ecology: 'the total science of the connections of the organism to the surrounding external world' (Haeckel 1866; Egerton 2013). See (Ings & Hawes 2018) for other important naturalists, ranging back to the ancient Greeks.

Henceforth, the interplay of environmental constraints, unavoidable organismal 'trade-offs'[2] and the competition for resources were disclosed as the main drivers of biodiversity and formed the cornerstones of the research scientists conducted in the following time (Tilman 1990).

The idea that environmental constraints affect biodiversity was derived from the observation of biodiversity patterns (Hutchinson 1959; Gaston 2000). These patterns include the 'latitudinal diversity gradient', the finding that biodiversity is generally higher in the tropics compared to temperate or boreal regions (Mittelbach et al. 2007), and the 'species-area' relationship, the finding that biodiversity generally increases with the size of habitable area (Rosenzweig 1995; Scheiner 2003). Biodiversity is also increased in places with decreased isolation from habitable areas (MacArthur & Wilson 1967; Kadmon & Allouche 2007), in places with heterogeneous environmental conditions (Stein et al. 2014), and in places where environmental conditions are benign for survival, growth and reproduction (cf. 'fundamental productivity' in Hutchinson 1959 , and 'species-energy' relationship in Evans et al. 2005b). Generally, biodiversity is increased at lower trophic levels[3] of a community[4] and when organisms are small in size (Elton 1927; Hutchinson 1959; Brown et al. 2004).

The idea that competition for resources among species could maintain biodiversity was identified in mathematical and experimental studies. Among the first theoretical frameworks was the principle of 'competitive exclusion' (also known as the 'Volterra-Gause principle'; (Lotka 1920; Volterra 1926; Gause 1934; Hutchinson 1959; Hardin 1960). The principle of competitive exclusion states that when several species compete for the same resources, eventually the most efficient species outcompetes all its fellow campaigners (Hardin 1960; Hutchinson 1961; Leibold 1995). In the light of this principle the concept of the niche (Grinnell 1917; Elton 1927; Hutchinson 1957; Macarthur & Levins

[2]A trade-off signifies that resources allocated to one trait cannot simultaneously be allocated to other traits and hence, allocations to one trait beneficial for one environmental constraint necessarily decrease the ability to cope with other environmental constraints (Tilman 1990).

[3]A trophic level corresponds to the functional role an organism has in a community in terms of its food relationships to other organisms. The trophic levels in a typical community are primary producers, herbivores, predators, carnivores and decomposers (Lindeman 1942).

[4] A community refers to an association of interacting organisms of different species that share the same place and time (Möbius 1877).

1967; Vandermeer 1972; Hutchinson 1978) was used to explain the existence and stability of biodiversity (Hardin 1960; Leibold 1995). A niche can be seen as the set of resources used by a species (Hurlbert 1981). In the perspective of the competitive exclusion principle, different species can coexist if they escape competition (and competitive exclusion) via the specialization on different sets of resources.

Therefore, it was postulated that a biological community can contain as many species as there are available niches, which equals the number of essential resources on which species can specialize (Hutchinson 1961). However, most observed biodiversity patterns do not conform to this postulate. Biodiversity is usually much higher than would be expected. The finding of inexplicably high numbers of species even among very similar organisms that all compete for the same resources became known as the 'Paradox of the Plankton' (also known as 'Hutchinson's paradox'; Hutchinson 1961). Explaining biodiversity has proven to be a hard nut to crack, as was pointed out by Hutchinson in his pioneering work 'Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?' (Hutchinson 1959) and one century after the influential writings of Humboldt, Darwin and Wallace, biodiversity still represented a veritable mystery (Tilman 2015).

In the subsequent time, new concepts were developed to explain high biodiversity via local interactions among species: an important idea is the theory of 'R*' (also known as the 'resource ratio hypothesis') originally proposed by (Macarthur & Levins 1964) and developed by Tilman (Tilman 1982). In this framework, the spatial (and temporal) heterogeneity in resource supply can foster the coexistence of a potentially unlimited number of species with different niches (Tilman 1982; Tilman 2011; Tilman 2015). Another important idea is the 'neutral theory', in which a high number of species can coexist by purely stochastic population dynamics of species that do not differ in their niches, so that their competitive ability and their effects on one another are identical (Bell 2001; Hubbell 2001). The 'contemporary coexistence theory' (Chesson 2000; Adler et al. 2007) states that both niche-based (so called stabilizing) mechanisms that reduce interspecific competition and neutral (so called equalizing) mechanisms that align interspecific competitive ability are important drivers of biodiversity. Additionally, biodiversity does not only depend on direct competitive (i.e. negative) interactions, but can be promoted by positive interactions among species (cf. 'facilitation'; (Bertness & Callaway 1994; Brooker et al. 2008), and via multiple indirect interactions that emerge in complex, multi-trophic ecological networks (Levine et al. 2017).

Besides local species interactions, also spatial mechanisms govern biodiversity: by considering the spatial context, it was found that local biotic communities are connected to other communities via organism dispersal and form so called 'meta-communities' (Wilson 1992; Hanski 1997; Leibold *et al.* 2004). In a spatial context, local biodiversity is referred to as α-diversity and is distinguished from the spatial dissimilarities among communities (β-diversity). Local α-diversity and spatial β-diversity add up to the total regional biodiversity (γ-diversity, Whittaker 1972). A variety of spatial mechanisms are important for biodiversity. For example, local biodiversity depends on species immigration, which can prevent the competitive exclusion of poor competitors in a local patch (cf. 'mass effect', Leibold et al. 2004; Holyoak et al. 2005). Local biodiversity also depends on the regional species pool (HilleRisLambers *et al.* 2012) and on the order in which species disperse to a local patch (cf. 'priority effect', Fukami & Morin 2003). In the 'species-sorting' framework, spatial heterogeneity in the environment allows for species with differential adaptions and the sustained colonization of habitats even if they undergo environmental change (Leibold *et al.* 2004; Logue *et al.* 2011). Spatial heterogeneity of the environment is a key driver of all spatial mechanisms governing biodiversity because it defines the functional connectivity that facilitates organism dispersal (Mouquet *et al.* 2006; Tscharntke *et al.* 2012; Thompson & Gonzalez 2016) and generally increases biodiversity of the regional species pool (Stein *et al.* 2014).

Besides local species interactions and spatial mechanisms, biodiversity ultimately depends on the evolutionary mechanisms speciation and extinction, which can be affected by environmental conditions (Mittelbach et al. 2007; Rabosky 2009; Cornell 2013). These evolutionary mechanisms explain many observed biodiversity patterns: for example, species extinction probabilities generally decrease with the amount of available energy or resources, because these conditions allow for a higher number of individuals in a species' population (Brown et al. 2004; Evans et al. 2005a; Cornell 2013; Storch et al. 2018). This explains why species diversity is usually elevated among smaller-sized organisms and among organisms of lower trophic levels, which are typically less affected by energy loss during energy conversion from one trophic level to another (Hutchinson 1959; Brown 1981; Brown et al. 2004). Larger population sizes and consequent decreased extinction probabilities also explain why species diversity generally increases with the size of habitable area and with the frequency of immigration fostered by decreased isolation (MacArthur & Wilson 1967; Cornell 2013). The probability of speciation events can also be

increased directly, for example by benign climatic conditions such as found in the tropics, which promote high rates of metabolic processes (Brown et al. 2004; Evans et al. 2005b) or by environmental heterogeneity, which provides a variety of niches to specialize in (Rosenzweig 1995; Cornell 2013).

Thus, as of now, many observed biodiversity patterns can be explained and much of Hutchinson's paradox has been resolved (Tilman 1982, 2015), at least theoretically. However, in most established frameworks the focus lays either on local species interactions and spatial mechanisms or on evolutionary processes separately, and the quest for a unified theory of biodiversity has proven to be difficult (Marquet et al. 2014). Often, empirical evidence for theoretically predicted mechanisms is lacking, such as the specific nature of trade-offs governing species coexistence in competitive communities (HilleRisLambers et al. 2012; Tilman 2015). Also, there is still considerable debate on how biodiversity relates to productivity, which is often used as a surrogate for energy availability (Gillman & Wright 2006). The finding that species' population sizes in the tropics are usually smaller than in temperate zones suggests that mechanisms governing biodiversity include more than only population-size dependent extinction rates (Storch et al. 2018). It is still not well understood why the history of life has been coined by coexistence rather than by competitive exclusion (Cornell 2013; Tilman 2015). Uncertainties are so large that it is even not clear whether biodiversity is restricted by ecological constraints (i.e. 'bounded') or if it would accumulate indefinitely if given enough time (i.e. 'unbounded', Cornell 2013). There are good reasons to assume that biodiversity is limited by ecological constraints, such as minimal population size per species and competitive exclusion by very similar species. These constraints should lead to higher extinction rates with higher preceding biodiversity (Emerson & Kolm 2005; Rabosky 2009). However, there are also good reasons to assume that extinction rates lower and speciation rates increase with higher preceding biodiversity, because a diverse community provides more potential niches to specialize on, stronger natural selection pressures (Tilman & Snell-Rood 2014; Zuppinger-Dingley et al. 2014), and a higher chance of present organisms that can actually adapt to these niches (Hutchinson 1959; Emerson & Kolm 2005; Cornell 2013).

Given all these arguments, we must conclude that biodiversity remains that fascinating marvel we still do not fully grasp.

Biodiversity loss in the Anthropocene: the sixth mass extinction

All organisms, including humans, modify their environment (Smith 2007). Who would have thought that human modifications could escalate through time so that today, they exert a major force on the biosphere (Ceballos et al. 2015)? How did *Homo sapiens* become the ultimate ecosystem engineer (Smith 2007)?

Behaviorally modern *Homo sapiens* emerged ~200,000 years ago (Klein 2008), spread out of Africa more than 50,000 years ago (Klein 2008), and had colonized the majority of the continents by ~12,000 years before present (B.P.; Goldewijk et al. 2010). This time marks the transition from the epoch of the cold Pleistocene to the climatically stable and warm Holocene (Goldewijk et al. 2010; Waters et al. 2016). Already during this time, human hunter-gatherer societies affected the biosphere via landscape burning, the extinction of more than half of Earth's mammalian megafauna, and their cascading effects on ecosystems (Ellis 2015). Ever since, human populations and resource consumption have grown tremendously, technological development increased, and human impacts on the ecosystems on Earth have sky-rocketed (Vitousek et al. 1997; Waters et al. 2016). Human signatures were propelled by the advent of agriculture (~11,000 years ago; Diamond 1997), Columbus' arrival in the Americas (1492; Columbus & de Las Casas 1991), the Industrial Revolution (~1760-1830; Berrill & Ashton 1949), and lately by the Great Acceleration (since ~1950; Waters et al. 2016). Most significant human signatures include land transformations such as deforestation, expansion of agricultural fields and urban areas, alterations of the biogeochemical cycles such as of carbon, nitrogen, phosphorous and water, the appearance and increased emission of manufactured materials, such as aluminum, plastics, concrete and synthetic organic chemicals, as well as biotic changes such as species introductions, domestications and extinctions (Vitousek et al. 1997; Ellis et al. 2010; Waters et al. 2016).

By the year 2000, most once-pristine ecosystems have been replaced by human-dominated landscape mosaics, (cf. 'Anthropogenic biomes' or 'Anthromes', Ellis & Ramankutty 2008), where biological communities are heavily shaped by and respond to anthropogenic activities. These 'Anthromes' cover ~76% of the ice-free terrestrial biosphere, of which 39% are in direct use for agriculture and settlements (Ellis & Ramankutty 2008; Ellis et al. 2010). The majority of "wild" biomes (i.e. without human settlements or substantial land use) are located in cold and dry areas (Ellis et al. 2010).

The human impacts on planet Earth changed the functioning of the Earth system so profoundly and pervasively, that unique traces in the stratigraphic record are visible at least since ~1950. This qualifies our time as a new epoch, the Anthropocene (Crutzen 2002; Waters et al. 2016).

The most significant consequences of human activities in the Anthropocene entail not only direct perturbations of climate dynamics (Oreskes 2004) and ecosystems (Vitousek et al. 1997; Tilman et al. 2001; Foley et al. 2005) but also dramatic rates of biodiversity loss (Pimm et al. 1995; Dirzo & Raven 2003; Pimm et al. 2014). The main causes of biodiversity loss are habitat loss, nitrogen pollution, climate warming, overexploitation (e.g. hunting, fishing) and trafficking of species to different habitats (Vitousek et al. 1997; Sala et al. 2000; Butchart et al. 2010).

Evidence suggests pre-human, 'background' extinction rates of around 0.1 per million species per year (0.1 E/MSY; Pimm *et al.* 1995; Ceballos *et al.* 2015). Extremely conservative estimates range up to 2 E/MSY (Ceballos et al. 2015). Current species losses average at around 100 E/MSY, which is 1000 times higher than the likely background rate and still 50 times higher than very conservative estimates. Extinction rates are projected to increase another 10-fold during the current century (MA 2005). Over the past 500 years alone, 10-64% of known species went extinct in the wild and a 75% extinction magnitude typical for so called 'mass extinction events' could be reached within less than 3 centuries (Barnosky et al. 2011). The rates of the current biodiversity loss are as high or even exceed extinction rates of the 'Big Five' mass extinction events preceding human existence, which substantiates the notion that the sixth mass extinction in the 4.5 billion year history of the Earth is underway (Barnosky et al. 2011; Ceballos et al. 2015).

This drastic extinction event is not only characterized by species losses but also by the spatial homogenization of biotic communities across landscapes around the globe (McKinney & Lockwood 1999; Olden & Rooney 2006; Baiser et al. 2012). The process of biotic homogenization, where a few cosmopolitan, rather generalist species expand their ranges to replace many local, often specialized, species, entails an increased genetic, taxonomic and functional similarity of communities across landscapes and regions (McKinney & Lockwood 1999; Olden & Rooney 2006), which profoundly affects the ecology and evolution of these communities (Olden et al. 2004).

The specific set, the number and kinds of organisms interacting with abiotic pools of energy and matter determine ecosystem structures and processes (Chapin et al. 2002).

Because ecosystem structures and processes foster functions and services essential for human well-being (de Groot et al. 2002; Foley et al. 2005; MA 2005; Mace et al. 2012), the dramatic impoverishment of the biosphere by both biodiversity loss and spatial homogenization poses one of the greatest threats to humanity (Chapin et al. 2000; Olden et al. 2004; Naeem et al. 2012).

This finding imposes a certain imperative to take a closer look not only at how species coexist, but how this coexistence in turn affects the functioning of the systems these very species compose. Or – in other words – what are the consequences of biodiversity loss for ecosystem functioning, services and ultimately human well-being?

Consequences of biodiversity loss: a biodiversity-ecosystem functioning (B-EF) perspective

In 1980 and the following years, awareness of the human dependence on the functions and services of ecosystems increased (Vitousek et al. 1986). It was also increasingly recognized that organisms not only respond to but actively shape environmental conditions (Jones et al. 1994; Chapin et al. 2002; Sterner & Elser 2002). These findings raised concerns over the dramatic magnitude of biodiversity loss (Ehrlich & Ehrlich 1981; Wilson 1988; Pimm et al. 1995) and scientists increasingly sought to answer a hitherto rarely asked question: What are the consequences of biodiversity loss for ecosystem functions, services and, eventually, human well-being (Cardinale et al. 2012)?

In 1991, a conference organized by Schulze and Mooney in Bayreuth, Germany and the following publication in 1993 (Schulze et al. 1993 ; with important contributions of Swift and Anderson, Vitousek & Hooper and McNaughton) and further studies by (Naeem *et al.* 1994; Tilman & Downing 1994; Tilman 1996; Hooper & Vitousek 1997; Hector *et al.* 1999) presented cases supporting the hypotheses of greater biodiversity leading to greater primary productivity, more efficient resource use and stability of ecosystems. These hypotheses formed the cornerstone of a growing amount of research in the field that became known as biodiversity-ecosystem functioning (B-EF) (Cardinale et al. 2011; Cardinale et al. 2012; Tilman et al. 2014).

B-EF research investigated if and how biodiversity affects whole-ecosystem structures, processes, functions and services. This implies a major shift of perspective on the concept of biodiversity: namely, from viewing biodiversity as a fascinating but insignificant

emergent property that is a mere byproduct of eco-evolutionary processes, to a perspective where biodiversity itself is a momentous characteristic of an ecosystem in which the number and kinds of organisms decisively determine structures and processes (Cardinale et al. 2011; Cardinale et al. 2012; Tilman et al. 2014).

Scientific and public interest in B-EF relationships grew dramatically in the following time, which is portrayed by several international initiatives focusing on biodiversity effects on ecosystems. For example, the United Nations Conference on Environment and Development (UNCED) in 1992 opened the Convention on Biological Diversity for signature, the international program dedicated to biodiversity science DIVERSITAS produced a global research agenda (Cardinale et al. 2012), and the Millennium Ecosystem Assessment summarized the state and trend of the world's biodiversity, ecosystem functions and ecosystem services (MA 2005). Initial disagreement and hot scientific debates around the existence and importance of biodiversity effects (Grime 1979; Huston 1979; Grime 1997; Huston 1997; Wardle 1999; Schmid 2002) were followed by a veritable explosion of studies investigating the issue (Cardinale et al. 2012). New knowledge in the field of B-EF was mainly gained via successive rounds of experimental studies in aquatic microcosms or grassland ecosystems (Schmid et al. 2002). In these experiments, the number and kinds of species were systematically manipulated to form well replicated communities orthogonal and balanced with respect to species richness and composition, while other environmental variables could be held constant (Schmid et al. 2002). Among the first influential and longest running of these biodiversity experiments are the ones at the Cedar Creek Ecosystem Science Reserve in Minnesota (cedarcreek.umn.edu; (Tilman 1996; Tilman et al. 2014), the Ecotron facilities in the United Kingdom and France (ecotron.cnrs.fr; imperial.ac.uk/cpb/history/theecotron/introduction; Naeem et al. 1995) the Jena Experiment in Germany (the-jena-experiment.de; Weisser et al. 2017), and the BIODEPTH project (https://www.cordis.europa.eu/project/rcn/31752_en.html; Hector et al. 1999).

Today, after >25 years of research, more than 600 experiments manipulating taxonomic, functional and genetic biodiversity (Purvis & Hector 2000; Violle et al. 2007), a large body of mathematical theory (Cardinale et al. 2012), several quantitative data syntheses (Balvanera et al. 2006; Cardinale et al. 2006; Cardinale et al. 2012) and consensus papers (Loreau et al. 2001; Loreau et al. 2002; Hooper et al. 2005; Cardinale et al. 2011; Cardinale et al. 2012; Tilman et al. 2014) have resolved much of initial

controversies around the importance of biodiversity. First, biodiversity unequivocally increases important ecosystem functions, such as the efficiency of essential resource capture, biomass production, matter decomposition and nutrient recycling. Second, biodiversity increases the temporal stability of ecosystem functions such as biomass production and increases the resilience (i.e. resistance and recovery) of ecosystems faced with pathogens (Civitello et al. 2015), invasions (Balvanera et al. 2006; Cardinale et al. 2012), and climate extremes (Isbell et al. 2015 ; see Ives & Carpenter 2007 for further forms of ecosystem stability). The relationship of biodiversity and a specific ecosystem function typically is positive but shows a decelerating increase at higher biodiversity levels (Cardinale et al. 2012). Positive relationships between biodiversity and measures of multiple ecosystem functions tend to be linear (Hector & Bagchi 2007). The positive biodiversity effects on ecosystem functions can be generated by niche differences among species, which lead to complementary resource use, reduced competition, increased facilitation and/or reduced pathogen pressure in the ecological community forming an ecosystem. Positive biodiversity effects can also be facilitated by so-called 'sampling' (also referred to as 'positive selection') effects that manifest in the increased chance of a well-functioning species being present and dominant in a community (Loreau & Hector 2001; Hooper et al. 2005; Cardinale et al. 2012; Tilman et al. 2014). The positive biodiversity effects on the stability of ecosystem functions are generated via the desynchronized dynamics of species populations (Yachi & Loreau 1999; Lehman & Tilman 2000; Isbell et al. 2009; Loreau & de Mazancourt 2013). Desynchronized dynamics can emerge when species have distinct niches and population declines in one species are compensated by population increases in another (Gonzalez & Loreau 2009). Another mechanism promoting desynchronized dynamics is the stochastic portfolio effect that emerges via the statistical averaging of the idiosyncratic species population dynamics at the level of the whole community (Doak et al. 1998; Hooper et al. 2005; Gross et al. 2014; Schindler et al. 2015). Additionally, positive biodiversity effects on ecosystem functions leading to the 'overyielding' of mixtures compared to monocultures (Tilman 1999; Schmid et al. 2008) can contribute to ecosystem stability, by disproportionally strongly increasing the mean compared to the variance of ecosystem functioning (de Mazancourt et al. 2013; Loreau & de Mazancourt 2013).

Hence, strong evidence supports the view that biodiversity loss potentially has dire consequences for ecosystem functioning, ecosystem services and hence, human well-

being (Cardinale et al. 2012; Tilman et al. 2014). However, because most of this evidence was derived from relatively simple, experimental systems, there is still incredible uncertainty about the actual consequences of biodiversity loss in the “real world”, where the services of much more complex ecosystems sustain the human existence (Lepš 2004; Duffy 2009; Brose & Hillebrand 2016). Biodiversity loss may already well have exceeded what has been called a “safe operating space for humanity”, which could destabilize critical biophysical systems on Earth and trigger deleterious, abrupt, and irreversible environmental changes (Rockstrom et al. 2009).

Thus, it is of utter importance to move the scope of B-EF research beyond simplified experimental settings to more realistic conditions of complex ecosystems at larger scales of space and time relevant for land management, ecosystem services, and human well-being (Lepš 2004; Srivastava & Vellend 2005; Thompson & Starzomski 2007; Duffy 2009; Brose & Hillebrand 2016; Wardle 2016).

From small-scale experiments to real-world landscapes: motivation & challenges

The halt of the ongoing biodiversity crisis is currently listed among the highest priorities on policy and land management action plans (see e.g. Intergovernmental Platform on Biodiversity and Ecosystem Services (2014) ipbes.net; Strategic Plan for Biodiversity 2011–2020 (2014); cbd.int/sp/targets/)

However, as of 2016, knowledge on specific consequences of biodiversity loss for the ecosystems that are being managed and that deliver valuable services to humans (Costanza et al. 2014), is still surprisingly limited (Lepš 2004; Srivastava & Vellend 2005; Thompson & Starzomski 2007; Duffy 2009; Brose & Hillebrand 2016; Wardle 2016).

These limitations are attributed to the fact that experimental settings of most B-EF studies strongly contrast with the conditions of non-experimental, natural or managed, so-called “real-world” (Duffy 2009) ecosystems. Specifically critical is that B-EF experiments have predominantly focused on newly assembled communities comprising species that were randomly chosen from a relatively small species pool, predominantly of a single trophic level (mostly primary producers of grasslands; Lepš 2004; Duffy 2009; Brose & Hillebrand 2016; Wardle 2016). The composition of these communities usually was maintained in a specific state via removal of unintended species (Schmid et al. 2002).

Furthermore, communities were held in homogeneous environmental conditions and were investigated over relatively short time-scales in relatively small study areas (typically less than 100 m^2; (Brose & Hillebrand 2016; Wardle 2016). Real-world communities, however, typically contain higher numbers of species from multiple trophic levels (e.g. primary producers, herbivores and carnivores) and larger pools of species (Brose & Hillebrand 2016). In these communities, species are typically connected by various direct and indirect interactions that form complex, multi-trophic ecological networks (Duffy et al. 2007; Levine et al. 2017). Species losses in these communities are not random but concern particular, typically rare or disturbance prone species, and can have cascading effects on the diversity of other species and trophic levels (Haddad et al. 2009; Wardle 2016). In the real world, fluctuations of the environment cause community composition to be “dynamic”, i.e. to be in a transient, non-equilibrium state of perpetual assembly and disassembly (Lepš 2004; Brose & Hillebrand 2016). Most importantly, such real-world communities form part of a heterogeneous patchwork of ecosystems that are constituted of biotic and abiotic, natural, and often anthropogenic elements exchanging energy, matter and organisms across the hydrosphere, biosphere, and atmosphere (Chapin et al. 2002; Heffernan et al. 2014; Walz 2015). This patchwork is usually referred to as landscape (Turner 1989; Pickett & Cadenasso 1995) but can be viewed as a meta-ecosystem (Loreau et al. 2003b). The meta-ecosystem framework expands the concept of meta-community by including abiotic components of ecosystems (i.e. not only organisms, but also energy and matter; Chapin *et al.* 2002; Loreau *et al.* 2003b). Independent of the specific framework, by shifting focus from isolated small-scale study areas to dynamic real-world landscapes, it becomes clear that local biotic communities are embedded in and interdependent on a specific context of environmental patterns and processes at various scales of space and time (Levin 1992; Tscharntke et al. 2012; Heffernan et al. 2014). Most of these patterns and processes were systematically excluded in typical B-EF experiments.

The most important challenges hampering a generalization of B-EF relationships from experimental plots to real-world landscapes are described below:

Context-dependence of biodiversity effects

Biodiversity effects in B-EF experiments are mainly attributed to local species interactions: for example, biodiversity effects on increased biomass production are attributed to increased resource-use via stochastic or niche-based resource-use

complementarity among species (Tilman *et al.* 2014). In real-world landscapes, not only local species interactions, but also spatial and evolutionary mechanisms of species coexistence (cf. page 19; HilleRisLambers et al. 2012; Leibold et al. 2017) affect local species diversity, species composition, species interactions and trait distributions (Lepš 2004; Tscharntke et al. 2012; Brose & Hillebrand 2016; Leibold et al. 2017). These mechanisms could lead to local communities that not necessarily consist of species with complementary resource-use, but of species with good abilities for dispersal, disturbance-resistance or species that were simply lucky to arrive at a local patch at a good moment (Fukami & Morin 2003; Leibold *et al.* 2004; Holyoak *et al.* 2005; Brose & Hillebrand 2016). Hence, local biodiversity effects on ecosystem functions such as biomass production might be decreased in such communities, as a result of the specific mechanisms of coexistence and the environmental context (Brose & Hillebrand 2016).

To date, the extent to which biodiversity effects depend on mechanisms of species coexistence (i.e. causes of biodiversity) and environmental context is largely unknown. Evidence from studies that observed B-EF relationships in non-experimental conditions is very inconsistent, which is likely due to the difficulty of disentangling the causes and effects of biodiversity in such scenarios (Grace 1999; Gillman & Wright 2006; Grace et al. 2007; Cardinale et al. 2009; Brose & Hillebrand 2016; Grace et al. 2016; Wardle 2016).

Relative importance of biodiversity effects

In several studies, it has been questioned if biodiversity effects on ecosystem functions are important compared to the severe effects of global change drivers such as land transformation, nitrogen pollution, pesticide use or CO_2 elevation, especially when larger spatial and temporal scales are considered (Srivastava & Vellend 2005; Grace et al. 2007; Hillebrand & Matthiessen 2009).

Recent evidence derived from experiments, however, suggests the opposite: studies by (Hooper et al. 2012) and (Tilman et al. 2012) found that biodiversity effects on ecosystem productivity and decomposition are comparable or even larger in magnitude than effects of climate warming, elevated CO_2 or nitrogen pollution, for example. Additionally, large parts of global change driver effects on ecosystem productivity and stability are actually not direct, but indirectly mediated via the loss of species they cause (Isbell et al. 2013; Hautier et al. 2015). Expanding the scope from experimental to real-world grasslands, (Allan et al.

2015) found that those land use effects that were indirectly mediated via biodiversity were as strong as direct effects of land use on ecosystem functions on average.

Biodiversity effects on underexplored ecosystem functions

The investigation of B-EF relationships in real-world landscapes demands the consideration of various ecosystem types beyond grasslands, such as forests, agricultural fields, and urban systems. The ensemble of these ecosystem types provides hitherto underexplored functions relevant to human well-being, such as climate regulation. For example, the structure and productivity of ecosystems can modulate surface physical properties such as albedo and roughness length, and affects carbon, water and energy fluxes (Oke 2002; McPherson 2007; Bonan 2008). Another important ecosystem function is the seasonal timing of species' life cycle events, generally referred to as phenology. Phenology is important for species interactions (Rathcke & Lacey 1985; Hooper 1998) and can indicate the ability of species and communities to adapt to climate change (Jump & Penuelas 2005; Cleland et al. 2012). The seasonal onset and offset of primary productivity in a landscape can further affect and be affected by climatic conditions (Menzel 2013; Garonna et al. 2014).

Biodiversity effects across scales

While previous research on B-EF relationships focused on small-study areas and local biodiversity (i.e. α-diversity; Whittaker 1972), little is known about the relative importance of spatial (i.e. β-diversity) and regional biodiversity (i.e. γ-diversity) for local and regional ecosystem functions and stability in dynamic real-world landscapes (Wang & Loreau 2014; Brose & Hillebrand 2016).

Theoretical considerations suggest that γ-diversity can act as a 'spatial insurance' for local ecosystem functioning via spatial exchanges of species with desynchronized population dynamics among local ecosystems (Yachi & Loreau 1999; Loreau et al. 2003a). The importance of these spatial exchanges for α-diversity and ecosystem functioning has been noted by many meta-population and landscape ecologists (Leibold *et al.* 2004; Holyoak *et al.* 2005; Logue *et al.* 2011; Tscharntke *et al.* 2012). For example, the spatial spillover of species into local habitats can mask or 'rescue' local biodiversity and ecosystem functions. This has been shown for local land-use intensification and

consequent decreases in local biodiversity and ecosystem functions that were masked by recolonization of species from the surrounding landscape in grasslands and crop fields (Tscharntke et al. 2012; Gamez-Virues et al. 2015; Baillod et al. 2017). The 'spatial subsidies' of organic and inorganic materials from the surrounding landscape can have similar effects (Polis et al. 1997; Polis et al. 2004).

All these effects, including spatial insurance effects of γ-diversity are critically dependent on the single characteristic specific enough to define a landscape: spatial heterogeneity (Turner 1989). Landscape spatial heterogeneity is determined by the composition and configuration of landscape elements (Duelli 1997; Turner 2005; Fahrig *et al.* 2011). Recent theoretical advances have found that the spatial dissimilarity among communities (β-diversity) contributes to regional stability of ecosystem functions via the asynchronous dynamics of different communities in a landscape (Wang & Loreau 2014, 2016). The spatial heterogeneity of both biotic and abiotic elements can directly increase regional ecosystem functioning and stability, by reducing the spatial correlation of environmental fluctuations (Moran 1953). In most real-world cases, abiotic and biotic components of ecosystems are intimately linked and should therefore be considered together (Chapin et al. 2002; Massol et al. 2011), which can be achieved in the concept of meta-ecosystems (Loreau et al. 2003b). In a meta-ecosystems perspective, it is conceivable that the spatial diversity of ecosystems can promote meta-ecosystem functioning and stability via complementarity in structure or in spatial exchanges of materials and energy, in analogy to the complementarity of species increasing functioning and stability of a community (Tilman et al. 2014). Hence, biodiversity effects might not only be important at the small scales of ecological organization (Jorgensen & Nielsen 2013; Isbell et al. 2017) such as species, but could also manifest at larger scales of ecological organization, such as entire habitats or ecosystems. Interestingly, this hypothesis is supported by a study of experimental aquatic microcosms (Alsterberg et al. 2017).

Thus, because the conditions in typical B-EF experiments contrast so strongly with real-world landscapes that include a myriad of processes not testable in such settings, it is still not clear if the established B-EF patterns and mechanisms are sufficiently general, important and hence, relevant for human well-being.

It is very likely that findings from B-EF experiments underestimate the importance of biodiversity for the functioning and services of real-world landscapes (Duffy 2009; Isbell et al. 2013): studies have shown that realistic extinction scenarios increased the magnitude of biodiversity loss compared to random scenarios (Petchey & Gaston 2002; Zavaleta & Hulvey 2004). Biodiversity effects in experiments also tend to increase with time (Cardinale et al. 2007; Reich et al. 2012) and sustaining multiple ecosystem functions requires more species than when only one function is considered (Hector & Bagchi 2007; Zavaleta et al. 2010). Hence, the true functional importance of biodiversity might lie in the maintenance of multiple ecosystem functions across times and places, especially if these places are faced with environmental perturbations (Brose & Hillebrand 2016; Isbell *et al.* 2018).

Therefore, it is high time to assess the relevance of biodiversity for the functions and services provided by real-world landscapes, in order to generate findings useful for land and policy management and hence findings that are relevant for human well-being.

Thesis outline

In this thesis, I aim to elucidate if biodiversity effects on ecosystem functions identified in small-scale experiments can be generalized to real-world landscapes. Therefore, I contribute knowledge on the generality of biodiversity effects and their importance for human well-being at scales relevant for policy and land management.

I adopt the perspective applied in biodiversity-ecosystem functioning (B-EF) experiments and therefore deliberately test for biodiversity effects on measures of ecosystem functions that I observe in real-world landscapes. However, B-EF relationships in real-world conditions are likely shaped by both causes and effects of biodiversity. To reduce the bias in observed B-EF relationships not due to biodiversity effects, I work with systematic study designs that allow statistically controlling for potentially confounding factors. I applied these study designs to data observed across Switzerland (Fig.1), which offers ideal conditions for this purpose because it spans large environmental gradients that occur over a relatively small spatial area.

Specifically, I tackle the following unresolved questions (as marked in bold in the previous section):

i) Are biodiversity effects dependent on environmental conditions?

ii) Are biodiversity effects important for ecosystem functions, compared to other environmental drivers?

iii) Is biodiversity important for underexplored ecosystem functions related to vegetation phenology and climate regulation?

iv) Can biodiversity effects be generalized across scales of space or ecological organization?

I investigate these questions in three chapters, in which I focus on different spatial scales:

In chapter 1, I analyze local tree diversity (α-diversity) and landscape diversity (β-diversity) effects on forest productivity and phenology. To investigate the generality of diversity effects, I test their interrelation with environmental context at local and landscape spatial scales. To assess the importance of diversity effects, I compare their magnitude to effects of environmental context variables. I use 36 forest sites that are replicated with respect to three forest types and six biogeographic regions. I measure tree diversity, forest productivity and phenology (approximated by leaf area index and growing season length, respectively) in situ during the time of 2015-2016 and derive landscape diversity and environmental context from geographic information data.

In chapter 2, I analyze if the spatial diversity of ecosystem types (β-diversity) is related to long-term functioning and stability of real-world landscapes. I assess the context and scale dependence of β-diversity effects and compare their magnitude to the magnitude of effects of other environmental drivers. I adopt classic study design principles from B-EF research (Schmid et al. 2002), where I sample sets of landscapes spanning orthogonal and balanced gradients in land-cover type richness, our proxy for β-diversity, from geographic information data. Profiting from high data availability, I selected over 4,000 landscapes with 250×250 m and 500×500 m area in 36 climatic and altitudinal blocks. I derive measures of landscape functioning related to primary productivity, vegetation phenology and albedo in the time of 2000-2016 from remotely-sensed information.

In chapter 3, I analyze how regional biodiversity (γ-diversity) is related to long-term functioning and stability of real-world landscapes. I assess the generality of γ-diversity effects by testing their interrelation with environmental context variables across a large altitude gradient. I compare the magnitude of γ-diversity effects to the magnitude of effects of environmental drivers and test if γ-diversity effects are mediated via these drivers. I use information on bird, plant and butterfly biodiversity for 447 landscapes 1 km^2 in size across Switzerland. I derive measures of landscape functioning approximating primary productivity and vegetation phenology, and their inter-annual stability and temporal trends from remotely-sensed information in the time of 2000-2015.

Finally, in the general discussion, I synthesize the results of my analyses, discuss questions i)-iv), limitations, and future directions.

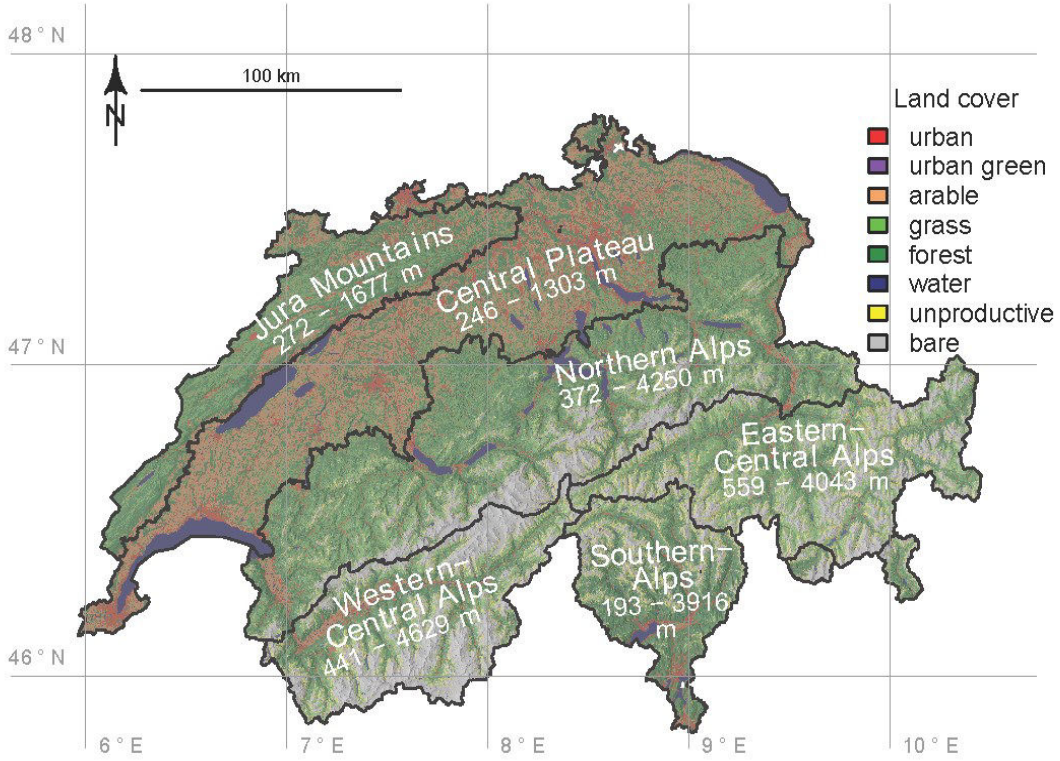

Fig. 1. **Study region.** Switzerland covers six biogeographic regions (BGR) that differ in flora and fauna, as well as climatic, topographic and edaphic conditions (Weber *et al.* 2004). Differences in BGR are also found with respect to land cover distribution (see legend). BGR boundaries are delineated with black color, names and altitude ranges in meters above sea level are written in white color.

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Chapter 1: Local and landscape-level diversity effects on forest functioning

Fieldwork in a Swiss forest. Photo: Rahel Furrer.

Local and landscape-level diversity effects on forest functioning

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Abstract

Research of the past decades has shown that biodiversity (B) is a fundamental driver of ecosystem functioning (EF). However, most of this B-EF research focused on experimental communities that were established on small areas where environmental context was held constant. If B-EF relationships can be generalized to natural or managed ecosystems that are embedded in variable landscape contexts remains unclear. Therefore, in this study, we investigated biodiversity effects on ecosystem functions of 36 forest stands that were replicated across vast environmental conditions in managed landscapes. We approximated forest productivity by leaf area index and forest phenology by growing season length and tested effects of tree species richness and land-cover type richness on these variables. We then examined the correlation and the confounding of local and landscape-level diversity effects with environmental context related to stand structure, landscape structure, climate, and topography. We found that tree diversity ranges among the most important determinants of forest leaf area index and growing season length of all tested variables. The positive tree diversity effects were remarkably consistent across the different environmental conditions we investigated and we found no indication of a context-dependent change in these diversity effects. Land-cover diversity was not directly related to local forest functions but could nevertheless be important via its positive relation to tree diversity.

Keywords: forest biodiversity and ecosystem functioning, leaf area index, canopy packing, growing season length, context-dependence, local and landscape spatial scales, moderation of biodiversity effects

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BS, JO, MB and PAN conceived the study
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Introduction

Biodiversity-ecosystem functioning (B-EF) studies of the past decades have revealed that biodiversity is an important driver of ecosystem functioning (Tilman *et al.* 2014). Most studies were concerned with effects on primary productivity, which integrates the efficiency of a community in capturing essential resources and converting these into biomass (Cardinale *et al.* 2012). To date, B-EF studies have predominantly focused on experimental communities with relatively small spatial extent and that were established in a relatively homogenous environment (Brose & Hillebrand 2016; Wardle 2016). This allowed to systematically identify causal effects of biodiversity, with positive decelerating responses of productivity to increasing species richness emerging as fairly general pattern.

The B-EF relationships identified in experiments largely encompass effects of local diversity that are driven by local mechanisms. To which extent the B-EF relationships found in experiments can be generalized to so called “real-world” (Duffy 2009) ecosystems in natural or managed landscapes remains largely unclear (Brose & Hillebrand 2016; Wardle 2016; Mori 2018).

Natural or managed landscapes provide functions and services of paramount importance to humans (Costanza *et al.* 2014). In these landscapes, ecosystems are connected by the exchange of energy, matter and organisms and thus form meta-ecosystems (Chapin *et al.* 2002; Loreau *et al.* 2003b; Walz 2015). In such meta-ecosystems, conditions at the local scale are strongly intertwined with the patterns and processes at larger scales of space, time and ecological organization (Levin 1992; Tscharntke *et al.* 2012; Heffernan *et al.* 2014). In other words, real-world ecosystems are embedded in a larger-scale context that typically is variable, unlike the situation usually realized in small-scale B-EF experiments. This larger-scale context may give rise to larger-scale mechanisms that potentially affect local biodiversity and ecosystem functions (Leibold *et al.* 2017). For example, species may disperse and colonize habitats in which they otherwise would not occur, thereby increasing local diversity (Leibold *et al.* 2004). Such spatial and demographic processes are not only important for plant but also for other taxa including consumers and pathogens (Duflot *et al.* 2014; Gamez-Virues *et al.* 2015; Perovic *et al.* 2015). Potentially important characteristics of landscape structure are the connectivity of habitats, the land use, climate, topography, and their spatial heterogeneity (Bertness & Callaway 1994; Mouquet *et al.* 2006; Tscharntke *et al.* 2012; Allan *et al.* 2015;

Leibold *et al.* 2017). All this complexity was purposely excluded from the plot-level experiments on which our current understanding of B-EF relationships largely rests.

In summary, we argue that it has become increasingly important to investigate B-EF relationships in human-dominated landscapes, which represent around 76% of the terrestrial biosphere (Ellis *et al.* 2010). Such studies of real-world B-EF relationships need to consider the larger scale landscape context of ecosystems, in addition to local species diversity. Here, we did so by studying leaf area index as indicator of productivity and growing season length as measure of phenology in 36 forest stands over a period of two years. These forest stands were systematically selected to cover three forest types. The study design was replicated in six distinct biogeographic regions that differed with respect to the regional species pool, climatic, topographic, and edaphic conditions (Wohlgemuth 1996). We quantified the extent to which our functioning metrics could be explained by a range of variables. At the local scale, we used species richness as primary predictor of ecosystem functioning because it is the key design variable in B-EF experiments. In analogy, at the landscape scale, we focused on land-cover type richness as predictor. We based our statistical models on these prioritized variables and then extended these with metrics that characterize further aspects of the local and landscape context of the selected forests plots. In addition to the explanatory power of species and landscape richness, we were interested in the overall correlation structure and the statistical confounding with environmental context variables related to landscape structure, stand structure, climate, and topography.

Materials and Methods

Study design

Using 36 forest stands, we analyzed the relationship of local measures of ecosystem functioning to local and landscape-level variables characterizing diversity and environmental conditions. These forest stands were a subset of sites that form an observation network of the Swiss biodiversity monitoring program (BDM, Z9 plot network, biodiversitymonitoring.ch; (Weber *et al.* 2004); Fig. 1). The sites formed a complete block design with the six biogeographic regions (BGR) as blocks and the forest types coniferous (>85% conifer individuals), broadleaved (<25%), and mixed (25-85%) within each block.

We randomly picked two replicates per forest type and block, with the constraint that 1) the sites were accessible, and 2) the sites represented one of 30 typical forests communities found in Switzerland (Table S1; (Delarze & Gonseth 2008); Jaccard similarities between plant species characteristic for these forest communities and the plant species monitored by the BDM). Based on the tree inventory we later conducted at each site, six of the 36 forests were reclassified and BGR and forest type therefore no longer fully orthogonal. At each site, we established a circular inventory plot with an area of 950 m^2.

Local forest diversity and stand structure

We marked all trees in each inventory plot with a diameter at breast height (DBH) of at least 5.5 cm and determined their species identity. The inventory revealed the presence of 2344 tree individuals belonging to 33 species (Table S2). Using this data, we determined tree density (n_{trees}: number of trees per plot), tree species richness (SR), rarefied tree species richness (n=21, which was the lowest number of trees found in any plot), plot-level stem basal area (BA), and an indicator combining stand age and demographic structure, the average basal area of the three largest trees (BA_{max}).

Landscape diversity, landscape structure, climate, and topography

We determined land cover composition around our plots using land cover classifications of points arranged on a 100m rectangular grid (product NOAS04, Swiss Federal Statistical Office, GEOSTAT). We aggregated the original 17 land-cover types into the classes forest, meadow, urban, arable, water, urban green, bare land (e.g. scree slopes), and unproductive (e.g. ruderal areas). Using this grid data and “Fragstats” (McGarigal 2015), we determined land cover type richness (LR), patch density (PD), and edge density (ED) in circular areas with radii varying from 100m to 6400m. LR was most variable among 600m radius landscapes, and we therefore used these metrics for all our analyses. We further calculated a measure of forest connectivity (F_{conn}; named “cohesion” in Fragstats) and the fractional cover of forest in the landscape (F_{frac}).

We characterized landscape-level topography by average altitude, slope, and the N-aspect of the slope based on a digital elevation model (product DHM25, Swiss Federal office of Topography: swisstopo). As indicators of climate, we used average mean annual temperature and annual precipitation (years 2000—2017, products TabsM and RhiresM, Swiss Federal office of Meteorology and Climatology: MeteoSwiss).

Ecosystem functioning

Productivity

We determined peak-season leaf area index (LAI) in summer 2015 and 2016. In each forest inventory plot, we recorded digital hemispheric photographs (DHP) at three random locations. The camera (Nikon D90, Sigma 4.5mm f/2.8 circular fish eye lens, ISO 200) was mounted on a tripod 1m above ground pointing vertically upwards. To achieve even illumination of the sky, we took the photos under overcast conditions or at dusk or dawn. DHPs were pre-processed using a custom software (unpublished) to correct for remaining gradients in sky brightness and LAI calculated with Hemisfer 2.1 (Schleppi et al. 2007) with algorithms correcting for slope (Norman & Campbell 1989) and clumping (Chen & Cihlar 1995). We averaged the three LAI measurements per plot and then per year.

Phenology

In each plot, we installed an automatic light logger (HOBO UA-002-64; Onset Computer Corporation, Bourne, MA) 40 cm above ground with the sensor facing vertically upwards. A second logger was placed as close as possible to the plot but outside the forest canopy with no objects obstructing the light measurement. We fitted the loggers with a short-pass filter (cut off at 716 nm, KG1 716FHC6565, Knight Optical Ltd., Kent, UK) to only record photosynthetically active radiation (PAR; 400 nm – 700 nm). The sensors were calibrated in the laboratory using an integrating sphere (RTS-3ZC; ASD Inc., Longmont, CO) and a spectroradiometer (FieldSpec 4 Standard-Res; ASD Inc., Longmont, CO). Illuminance (Lux) was recorded half hourly from spring 2015 until autumn/winter 2017 (Fig.S1). We determined the attenuation of PAR as one minus the ratio of daily average inside and outside recordings (11 to 16h). These time series were smoothed by fitting a cubic spline (15 degrees of freedom) before determining start (SOS) and end (EOS) of the growing season in every year. SOS was defined as date at which illuminance attenuation first exceeded the mean of annual minimum and maximum. Conversely, EOS was determined as final date at which attenuation remained about this threshold. Growing season length (GSL) was calculated as EOS minus SOS (Fig.S1).

Data analysis

We first assessed the overall correlation coefficients (r) among variables characterizing local and landscape diversity, landscape structure, topography, climate, stand structure, and forest ecosystem functioning. We evaluated the strength of these correlations

according to (Cohen 1988), where effects are small, medium and large for r=0.1, r=0.3 and r=0.5, respectively. Based on this initial assessment, which we verified using principal component analysis (Fig. S2), we selected representative, largely independent, candidate predictors of ecosystem functioning. As indicator of landscape structure, we used edge density (ED), which was highly correlated with patch density (PD), forest connectivity (F_{conn}), and forest fraction (F_{frac}). We further selected altitude (alt.), which was indicative also of mean annual temperature (temp.). We kept precipitation (precip.) because it was relatively independent of the other variables. Finally, we used the number of trees (n_{trees}) in the plot to characterize forest stand structure. Because we could adjust for n_{trees} in our models, we focused on species richness instead of rarefied species richness in our analyses. We always kept the factors biogeographic region (BGR) and forest type (FT) because they were the basis of our plot selection.

Using these predictors, we modelled the ecosystem functioning metrics LAI and GSL. Their predictive power was assessed by variance partitioning (method by (Lindeman *et al.* 1980) as implemented in the "lmg" function of the R library "relaimpo"). We further assessed the variance explained by these predictors when fitted alone and when data were first adjusted for all other predictors.

Finally, we tested effects of local tree species diversity (SR) and landscape diversity (LR) on ecosystem functioning, adjusting separately for each of the other selected predictors. For these models, we determined the effect sizes for SR and LR as partial correlations derived from F-ratios:

$r_{partial} = \sqrt{\frac{F}{F+df_{error}}}$ (Rosenthal 1994; Hullett & Levine 2003).

Results

Correlation of local and landscape predictors of ecosystem functions

Tree species richness (SR; local scale) correlated significantly positively (r=0.38, P<0.05) with land-cover type richness (LR; landscape scale; Fig.2). Edge density (ED), patch density (PD), the fraction of forested area (F_{frac}), and the connectivity of forest patches (F_{conn}) formed a highly correlated complex (|r|>0.63, P<0.001 for all pairs).

Interestingly, these variables correlated with LR (range |r|=0.23-0.69, all P<0.01 except F_{conn}: n.s.) but independent of SR (range |r|=0.02-0.09, all n.s.). In other words, LR captured some essence of both SR and these other landscape-level structural metrics.

Of the topographic and climatic variables (Fig 2), altitude and temperature were, not surprisingly, highly correlated. Temperatures decreased with altitude (r=-0.86, P<0.001) and were lower on north-exposed and steep slopes (r=-0.34, and r=-0.35, both P<0.05). Precipitation was not significantly related to these variables.

At the stand level, the size of the largest trees (BA_{max}), which we consider a proxy of stand age, correlated positively with plot basal area (BA; r=0.72, P<0.001) and negatively with the number of trees (n_{trees}; r=-0.59, P<0.001).

There was little correlation among variables of different groups. Exceptions were SR which correlated positively with temperature and negatively with altitude (r=0.45, and r=-0.47, both P<0.01), and n_{trees} which increased with LR, ED and PD (range r=0.33-0.4, all P<0.05; Fig. 2).

Testing the relationship of ecosystem functioning with diversity variables, we detected significant correlations only between SR and leaf area index (LAI; r=0. 37, P<0.05; Fig.2). The correlation coefficient between SR and GSL also was positive but not significantly so (r=0.38, P<0.1). LR was unrelated to both LAI and GSL. The only other statistically significant correlations we found were between LAI and precipitation (r=0.37, P<0.05) and of GSL with temperature and altitude (r=0.80 and -0.83, P<0.01 for both).

Variance explained in ecosystem functions

SR ranged among the most important predictors of LAI in models containing eight selected variables (Fig. 3). Depending on sequential order, i.e. for which variables the effect was first adjusted, SR explained 9.5-14.0% of the overall variance. The amount of variance explained by SR exceeded the one of all the other variables except BGR, which figured as block in our study design.

A similar picture presents for GSL, with a similar amount of variation explained by SR (0.5-14.5%). The main difference between the two analyses was that altitude and BGR explained a very large fraction of the overall variance (8-70% and 10-43%, respectively), as was to be expected because GSL strongly decreases with temperature.

Landscape richness (LR), landscape structure (represented by ED), and stand structure (represented by n_{trees}) were not important in any model (Fig. 3).

Effects of species and landscape diversity, adjusted for environmental context

Using models explaining LAI, we found effect sizes ($r_{partial}$) of SR that remained high, independent of whether data were first adjusted for the other variables (range $r_{partial}$: 0.27-0.41; Fig. 4). Values of $r_{partial}$ exceeded 0.3 except in models first adjusting for altitude or forest type (lower SR in coniferous forests, $P<0.05$) in which case $r_{partial}$ was slightly lower. Importantly, high $r_{partial}$ values >0.3 were restored when data additionally were adjusted for the study design variable BGR (Fig.5).

In models of GSL, effect sizes of SR were similar as in models of LAI (Fig.4). However, effects of altitude were very large, and SR effects only became evident when including BGR in the model. With this adjustment, effects in fact became larger than for the analysis of LAI (range $r_{partial}$ of SR for LAI: 0.34-0.43 and for GSL: 0.47- 0.66, respectively; Fig.5).

Effect sizes for landscape richness (LR) generally were low and insignificant, although they increased in models of GSL when adjusting for BGR ($r_{partial}$: 0.34, n.s.; Fig.4; range $r_{partial}$ of LR for LAI: 0.05-0.15 and for GSL: 0.20- 0.42, respectively; Fig.5).

Discussion

We investigated the effects of local and landscape-level diversity and environmental context on forest functioning in managed landscapes. We found that local tree diversity, measured as species richness, was positively related to forest leaf area index and growing season length. Tree diversity explained on average more variance in these functions than the other variables related to landscape structure, climate, topography, and stand structure. Species diversity effects were relatively robust, with little confounding with the environmental context variables. Overall, our findings thus suggest that tree species diversity is an important driver of forest productivity and phenology, with effects that remain relatively constant across the range of environmental conditions encountered in managed landscapes. In contrast, landscape-level land-cover diversity showed little direct relation to local forest productivity and phenology. However, landscape diversity was strongly positively correlated to local tree species diversity. It may thus be that landscape diversity contributes to local ecosystem functioning indirectly through effects mediated by local species richness.

The positive tree species diversity effects we found on forest LAI are well in accordance with previous theoretical considerations (Morin et al. 2011) and empirical findings: positive tree diversity effects on "canopy packing" or "crown complementarity" were found in experimental (Pretzsch 2014; Schmid & Niklaus 2017; Williams *et al.* 2017) and non-experimental forest stands (Jucker et al. 2015). These effects were attributed to inherent differences of species in crown architecture, and to tree-neighborhood driven plastic responses in crown growth and vertical leaf distribution (Jucker et al. 2015; Niklaus et al. 2017; Williams et al. 2017). The increased crown complementarity with tree diversity demonstrates one of the first physically measurable rather than statistically inferred (cf. Loreau & Hector 2001) complementarity effects of biodiversity (Schmid & Niklaus 2017).

We found no significant relationship of tree species richness with basal area – if anything, this relationship was negative (correlation coefficient r=-0.23, n.s.), contrasting previous evidence (Baruffol *et al.* 2013; Vilà *et al.* 2013; Castro-Izaguirre *et al.* 2016). Whether diversity effects on basal area truly were absent or whether these were masked by unaccounted drivers remains unclear. Almost all Swiss forests are heavily managed by removing individual trees from stands, avoiding clear-cutting large areas. It may be that differences in management history among plots had a long lasting effect on basal area, whereas LAI recovered faster from such interventions. Thus, management history may have masked true biodiversity effects on stand basal area, whereas biodiversity effects on LAI were detectable. Independent of these considerations, our results suggest that productivity measured by leaf area index does not necessarily reflect productivity measured by woody biomass and that these two attributes are likely governed by different mechanisms. Hence, species richness effects on woody biomass production (Paquette & Messier 2011; Liang *et al.* 2016) might differ from species richness effects on the leaf area in forest stands.

Tree species richness correlated positively with both LAI and growing season length. Correlation coefficients were similar for both variables but the relationship only marginally significant for GSL. The reason for the lower statistical power in the case of GSL is that only 22 of the 36 forest sites showed a seasonal pattern in light attenuation (Fig.S1). For obvious reasons, GSL depended strongly on climate, and altitude and biogeographic region therefore were dominant predictors. Across our study sites, species richness correlated negatively with altitude, indicating that the two were confounded. This raised the possibility that tree species richness effects on GSL might in fact have been altitude

effects in disguise. However, we found that the opposite was true: the strong variation in GSL across biogeographic regions masked tree diversity effects. These increased substantially in magnitude and significance after we accounted for biogeographic region. Our findings of positive plot-level species richness effects on growing season length parallel earlier findings at the landscape scale (Oehri *et al.* 2017). Phenology plays an important role for species interactions (Rathcke & Lacey 1985) and the capability to adapt to environmental change (Jump & Penuelas 2005; Cleland *et al.* 2012). Hence, biodiversity might be important for the resilience of communities faced with global change under complex real-world conditions.

There is conflicting evidence whether landscape structure is important for local ecosystem functioning. In agricultural grasslands and crop fields, landscape heterogeneity increased local biological control (Tscharntke *et al.* 2012; Baillod *et al.* 2017). In tropical dry forest, landscape structure was less important for local above ground biomass (Luis Hernandez-Stefanoni *et al.* 2011). Our study suggests that landscape context is unimportant, but it is well possible that we have missed effects because of the scale mismatch between the area at which local ecosystem functions were measured (950 m^2) and the area at which landscape context was quantified (~ 1000 × 950 m^2). The forested area within the 600 m radius landscapes certainly was not homogeneous, and it is likely that the scale at which we derived landscape context was not the scale at which local forest conditions were influenced. It is well conceivable that at more similar scales of space, landscape diversity would have been related to ecosystem functioning (see examples from experimental and natural grasslands: (Aragon *et al.* 2011; Pasari *et al.* 2013; Hautier *et al.* 2018). In light of this scale mismatch, it appears all the more remarkable that land-cover richness was strongly related to local tree species richness in our study. This promotes the idea that environmental heterogeneity at larger scales drives local species richness (Stein *et al.* 2014). Importantly, this implies that landscape diversity can promote local ecosystem functioning indirectly, via positive effects on local biodiversity, which has been proposed in theoretical studies (Loreau *et al.* 2003a; Leibold *et al.* 2004) and is empirically supported (grassland and agricultural areas: (Tscharntke *et al.* 2012; Duflot *et al.* 2014; Gamez-Virues *et al.* 2015; Perovic *et al.* 2015; Baillod *et al.* 2017); forest: (Luis Hernandez-Stefanoni et al. 2011; Turner et al. 2013).

In our study, tree species richness effects stayed relatively constant when adjusting for different local and landscape environmental context variables. This suggests that

environmental context does not alter the local relationship between diversity and functioning. This reasoning is supported by the fact that we did not find significant interactions of tree species richness with environmental context variables in further exploratory analysis. The only exception was GSL, where species richness effects differed between forest types. However, this interaction was essentially due to coniferous forest plots for which season length was ill-defined. More generally, the potential dependence of biodiversity effects on environmental context remains poorly tested to date (Brose & Hillebrand 2016; Mori 2018). Experiments suggest that there is no such dependency (Hautier *et al.* 2015; Craven *et al.* 2016 ;but see Fridley 2002), whereas observational studies often suggest the contrary (Paquette & Messier 2011; Wu *et al.* 2015; Jucker *et al.* 2016; Liang *et al.* 2016; Ratcliffe *et al.* 2017). However, cause and effect of diversity often were not separated in the latter.

To conclude, we show that local tree species diversity is a powerful predictor of forest functions in managed real-world landscapes, similarly to the effects of species richness that have been found in B-EF experiments. Landscape diversity had only a low explanatory power, but was positively correlated with local species diversity and could thus exert important indirect effects. A general challenge in observational studies is to disentangle causes and effects of biodiversity (Mori 2018). Whereas the first addresses conditions that facilitate biodiversity, it is only the second that can identify the consequences of biodiversity loss for ecosystem functioning and ultimately, human well-being.

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Tables & Figures

Fig. 1

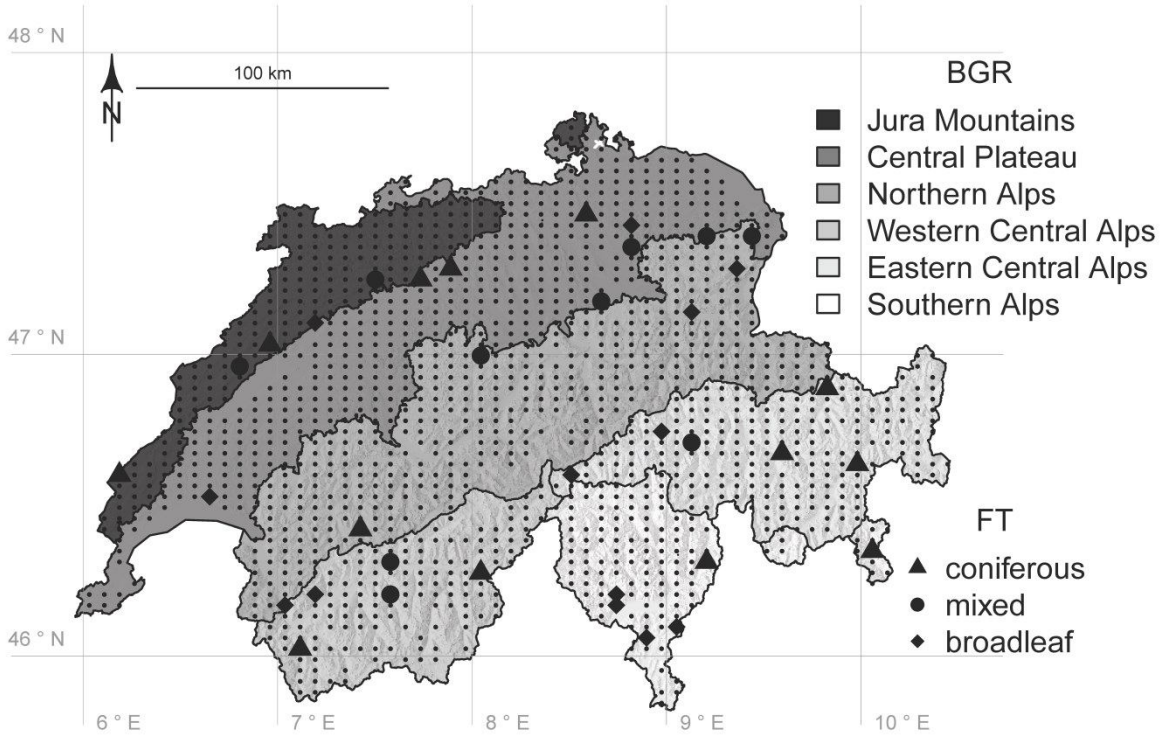


Fig. 1. **Study design.** From a total of 1416 BDM sites that are regularly spread across Switzerland (small black dots; BDM Z9 plot network; biodiversitymonitoring.ch) we selected 36 that we classified as "coniferous", "mixed" or "broadleaved" forests based on the Jaccard similarity of BDM-monitored plant communities to 30 typical Swiss forest plant communities (Table S1; Delarze & Gonseth 2008). We selected two replicates of each forest type (FT) in each of the six biogeographic regions (BGR) of Switzerland (Wohlgemuth 1996). We re-classified six forest types after executing the tree inventories, so that the final distribution of forest types is not fully orthogonal with BGR (triangles=coniferous forests, N=13; circles=mixed forests, N=10; diamonds=broadleaf forests, N=13).

Fig. 2

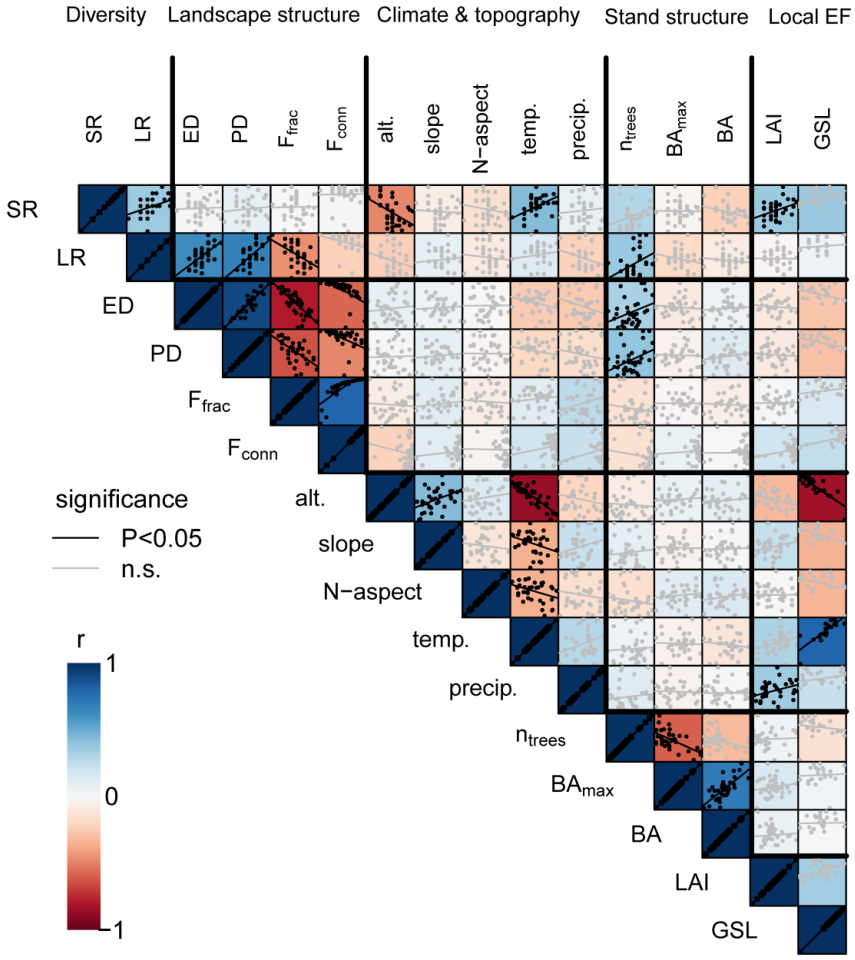


Fig. 2. **Correlations among local and landscape-level predictors of local ecosystem functions.** Significance (P<0.05) is indicated in black, sign of correlation is indicated with red to blue coloring (blue=positive correlation, red=negative correlation). We found positive correlations among local tree species richness (SR) with leaf area index (LAI; r=0. 37, P<0.05) and, marginally, with growing season length (GSL r=0.38, P<0.1). SR was also positively related to landscape-level land-cover richness (LR; r=0.38, P<0.05) but LR did not relate significantly to LAI or GSL. The landscape structure variables edge density (ED), patch density (PD), fractional cover of forest (F_{frac}) and connectivity of forest patches (F_{conn}) were highly correlated among each other and with LR, but showed no relationship with SR, LAI or GSL. The local stand structure variables (number of trees, n_{trees}; basal area, BA; and our proxy for forest age, BA_{max}) were correlated among each other but showed no strong relationship with SR, LAI or GSL. Of the climate and topography variables, temperature and altitude were strongly correlated and also showed significant relationships with SR and GSL. Precipitation was little related to other climate variables but showed a positive correlation with LAI (r=0.37, P<0.05). In general, the correlation among variables of different groups was not significant, with the exception of SR and n_{trees}. Number of study units n= 36 for LAI and n=22 for GSL.

Fig. 3

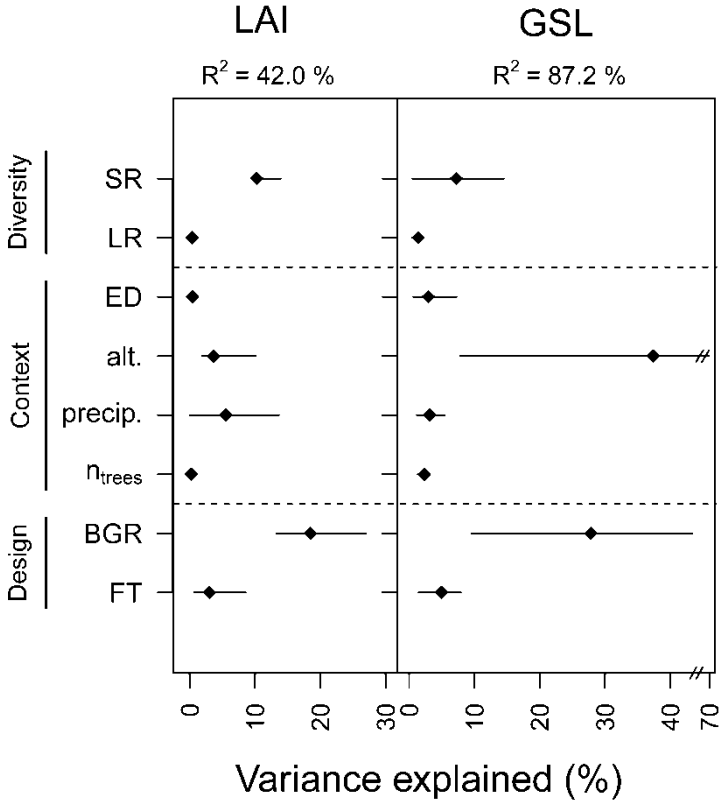


Fig. 3. **Variance explained in ecosystem functions by local and landscape-level variables.** Models containing the selected predictors relating to diversity, environmental context and study design explained 42% of variation in LAI and 87.2% of variation GSL. The R^2 contribution of every predictor averaged over all possible orderings in the model are indicated with dots, whereas lines connect the R^2 contributions when included last to R^2 contributions when included first in the model. SR was among the most important predictors and explained 10.3% of variance in LAI and 7.3% of variance in GSL on average (dots). The only variable exceeding the predictive power of SR in the case of LAI was the study design variable BGR (average R^2: 18.5%). In the case of GSL, altitude and BGR explained more variance than SR (average R^2: 37.4% and 27.8%, respectively). SR explained more variance in LAI and GSL than number of trees (n_{trees}; average R^2 LAI: 0.2%; GSL: 2.3%), forest type (FT; average R^2 LAI: 3%; GSL: 5%), and precipitation (precip.; average R^2 LAI: 5.5%; GSL: 3.2%). The landscape-level predictors land-cover richness (LR) and edge density (ED) generally explained little variance in LAI and GSL. Number of study units n= 36 for LAI and n=22 for GSL.

Fig. 4

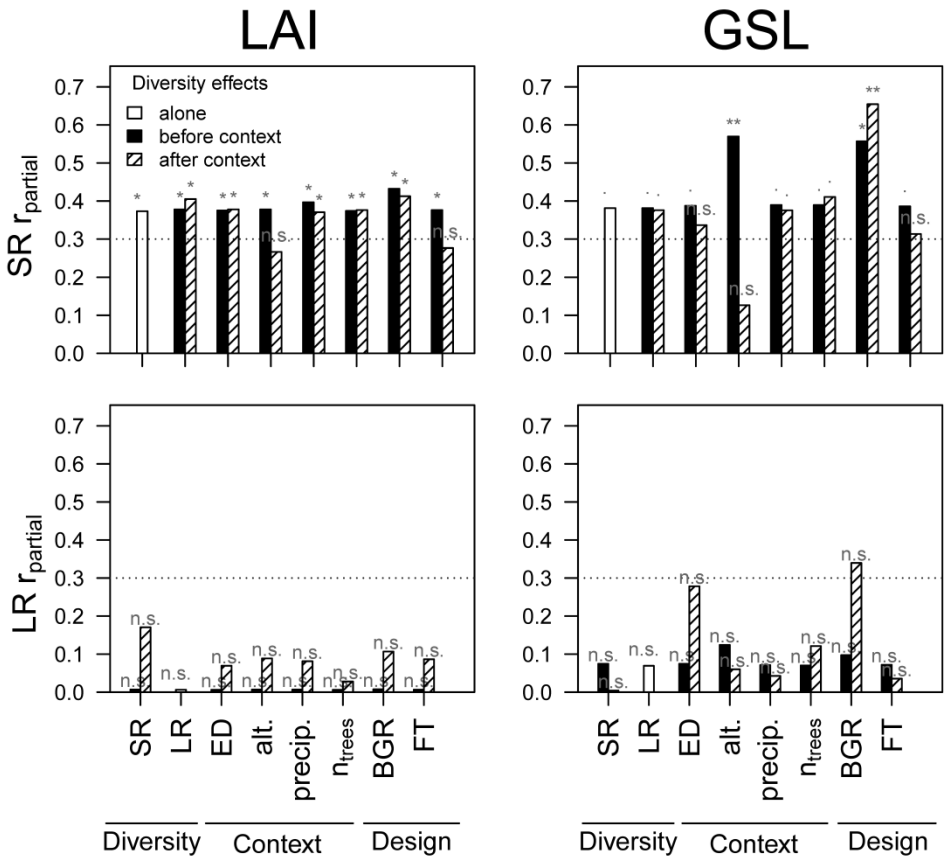


Fig. 4. **Effects of species and landscape diversity on local ecosystem functions, adjusted for environmental context.** We quantified effect sizes ($r_{partial}$) for local (SR) and landscape diversity (LR) in models where we included SR or LR only (open bars), in models where we included SR or LR before environmental context variables indicated on the x-axis (filled bars) and in models where we included SR or LR after these context variables (hashed bars). In the case of LAI, effect sizes of SR were relatively large (r>0.3) and similar in magnitude independent of the specific model (range $r_{partial}$: 0.37-0.41), except when we first adjusted for altitude (alt.; $r_{partial}$: 0.27) and forest type (FT) in the models ($r_{partial}$: 0.28). In the case of GSL, SR effect sizes were relatively similar in magnitude in most models (range $r_{partial}$: 0.31-0.41) but strongly decreased after adjusting for altitude ($r_{partial}$: 0.13), and strongly increased after adjusting for BGR ($r_{partial}$: 0.65). Effect sizes of LR generally were low and only increased to $r_{partial}$>0.3 in models where we first adjusted for biogeographic region (BGR) in the case of GSL. Significances: "***": P<0.001; "**": P<0.01; "*": P<0.05; ".": P<0.1; "n.s.": P>=0.1; number of study units n= 36 for LAI and n=22 for GSL.

Fig. 5

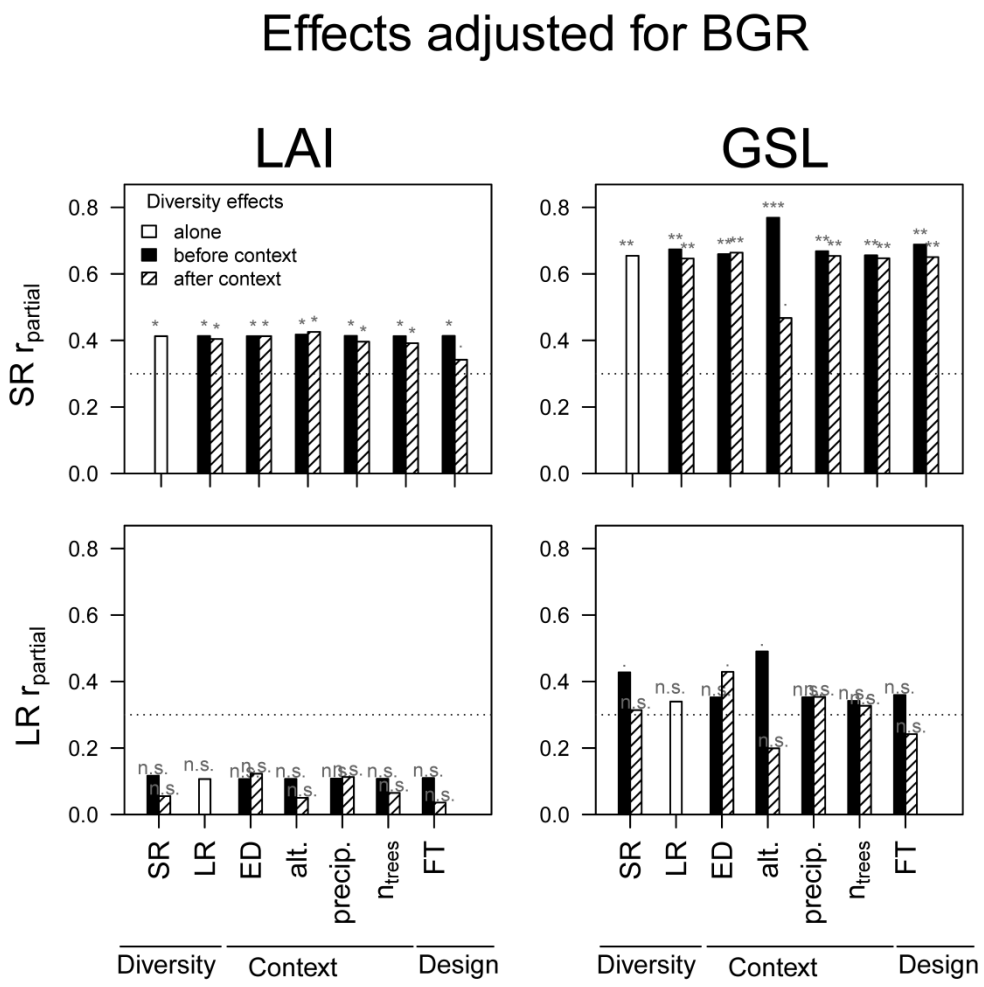


Fig. 5. **Effects of species and landscape diversity on local ecosystem functions, adjusted for BGR and environmental context.** We repeated all analyses with models that first adjusted for BGR. Hence, we derived effect sizes ($r_{partial}$) of local (SR) and landscape diversity (LR) in models where we included BGR and SR or LR alone (open bars), in models where we included BGR and SR or LR before environmental context variables on the x-axis (filled bars) or where we included BGR and SR or LR after these context variables (hashed bars). Effect sizes of SR in these models always exceeded 0.3 (range of $r_{partial}$ for LAI: 0.34-0.43 and GSL: 0.47- 0.66). Effect sizes of LR generally were low for LAI (range of $r_{partial}$: 0.05-0.15). In the case of GSL, effect sizes of LR ranged around 0.3 (range of $r_{partial}$: 0.31-0.43), except in the cases where we first adjusted for altitude (alt.: $r_{partial}$: 0.20) or forest type (FT: $r_{partial}$: 0.24) in the models. Significances: "***": P<0.001; "**": P<0.01; "*": P<0.05; ".": P<0.1; "n.s.": P>=0.1; number of study units n= 36 for LAI and n=22 for GSL.

Table S1. Forest communities found in Switzerland (Delarze & Gonseth 2008). We used the information on the typical species compositions of these forests to associate 1416 sites of the Swiss biodiversity monitoring program (BDM; biodiversitymonitoring.ch; Fig.1) with a likelihood of being a i) coniferous, ii) broadleaved or iii) mixed forest by using presence data of vascular plant species (Z9 Indicator of the BDM) and Jaccard's index of similarity.

Nr	Broad forest type	Specific forest community according to (Delarze & Gonseth 2008)	Most dominant plant species
1	i) coniferous	Molinio-Pinion	*Calamagrostis varia, Molinia arundinacea, Pinus sylvestris*
2		Erico-Pinion sylvestris	*Carex alba, Erica carnea, Picea abies, Pinus sylvestris*
3		Ononido-Pinion	*Arctostaphylos uva-ursi, Carex humilis, Pinus sylvestris*
4		Sphagno-Piceetum	*Picea abies, Vaccinium myrtillus*
5		Erico-Pinion mugo/uncinatae	*Erica carnea, Picea abies, Pinus mugo subsp. uncinata, Rhododendron hirsutum*
6		Abieti-Piceion	*Abies alba, Picea abies, Vaccinium myrtillus*
7		Vaccinio-Piceion	*Calamagrostis villosa, Picea abies, Vaccinium myrtillus*
8		Larici-Pinetum cembrae	*Larix decidua, Rhododendron ferrugineum, Vaccinium gaultherioides, Vaccinium myrtillus*
9		Junipero-Laricetum/Mélézin	*Larix decidua, Rhododendron ferrugineum, Vaccinium myrtillus, Vaccinium vitis-idaea*
10		Epilobion angustifolii	*Epilobium angustifolium*
11	ii) broadleaf	Alnion glutinosae	*Alnus glutinosa*
12		Salicion albae	*Salix alba*
13		Alnion incanae	*Alnus incana, Equisetum hyemale, Rubus caesius*
14		Luzulo-Fagenion	*Fagus sylvatica, Luzula luzuloides, Luzula nivea, Luzula sylvatica, Melampyrum pratense, Quercus petraea*
15		Lunario-Acerion	*Acer pseudoplatanus, Mercurialis perennis*
16		Tilion platyphylli	*Acer opalus, Corylus avellana, Mercurialis perennis, Tilia cordata, Tilia platyphyllos*
17		Carpinion	*Anemone nemorosa, Carex montana, Carex pilosa, Carpinus betulus, Festuca heterophylla, Quercus petraea, Quercus robur*
18		Quercion pubescenti-petraeae	*Acer opalus, Carex montana, Cornus mas, Hippocrepis emerus, Quercus petraea, Quercus pubescens*
19		Orno-Ostryon	*Cornus mas, Fraxinus ornus, Hippocrepis emerus, Ostrya carpinifolia, Quercus pubescens, Teucrium chamaedrys*
20		Quercion robori-petraeae	*Festuca heterophylla, Luzula nivea, Molinia arundinacea, Pteridium aquilinum, Quercus petraea*
21		Castanea sativa forest	*Castanea sativa, Festuca heterophylla, Luzula nivea, Molinia arundinacea, Pteridium aquilinum, Quercus petraea*
22		Betulion pubescentis	*Betula pendula, Betula pubescens, Molinia caerulea, Vaccinium myrtillus*
23		Fraxinion	*Fraxinus excelsior, Quercus robur*
24		Galio-Fagenion	*Allium ursinum, Anemone nemorosa, Arum maculatum, Circaea lutetiana, Fagus sylvatica, Galium odoratum,*
25		Atropion	*Fragaria vesca, Galeopsis tetrahit, Rubus idaeus*
26	iii) mixed	Cephalanthero-Fagenion	*Acer opalus, Carex alba, Carex flacca, Carex montana, Fagus sylvatica, Quercus petraea, Sesleria caerulea, Taxus baccata*
27		Dicrano-Pinion	*Calluna vulgaris, Pinus sylvestris, Vaccinium myrtillus*
28		Ledo-Pinion/Piceo-Vaccinienion uliginosi	*Pinus mugo subsp. uncinata, Vaccinium myrtillus, Vaccinium uliginosum*
29		Lonicero-Fagenion	*Fagus sylvatica, Galium odoratum, Lamium galeobdolon subsp. Montanum, Mercurialis perennis*
30		Abieti-Fagenion	*Abies alba, Adenostyles alliariae, Athyrium filix-femina, Fagus sylvatica, Hordelymus europaeus, Picea abies*

Table S2. List of all the tree species we found in the tree inventory, the number of individuals across all study sites and number of study sites with a respective species present.

Nr	Tree species identified in the tree inventory	Nr individuals	Nr study sites
1	Abies alba	99	13
2	Acer campestre	13	3
3	Acer platanoides	2	1
4	Acer pseudoplatanus	188	9
5	Alnus incana	81	1
6	Alnus viridis	8	2
7	Betula pendula	82	8
8	Carpinus betulus	1	1
9	Castanea sativa	127	3
10	Cornus mas	1	1
11	Corylus avellana	99	5
12	Fagus sylvatica	346	19
13	Fraxinus excelsior	89	14
14	Juglans regia	16	1
15	Juniperus communis	1	1
16	Larix decidua	38	10
17	Picea abies	665	26
18	Pinus cembra	35	2
19	Pinus sylvestris	56	2
20	Populus tremula	23	3
21	Prunus avium	68	8
22	Pyrus pyraster	1	1
23	Quercus petrea	25	5
24	Quercus pubescens	29	1
25	Quercus robur	5	2
26	Salix caprea	15	6
27	Sorbus aria	22	3
28	Sorbus aucuparia	145	5
29	Taxus baccata	2	2
30	Tilia cordata	23	1
31	Tilia platyphyllos	17	2
32	Ulmus glabra	15	3
33	Ulmus minor	7	1
	Total nr. of trees in inventory	2344	

Fig. S1

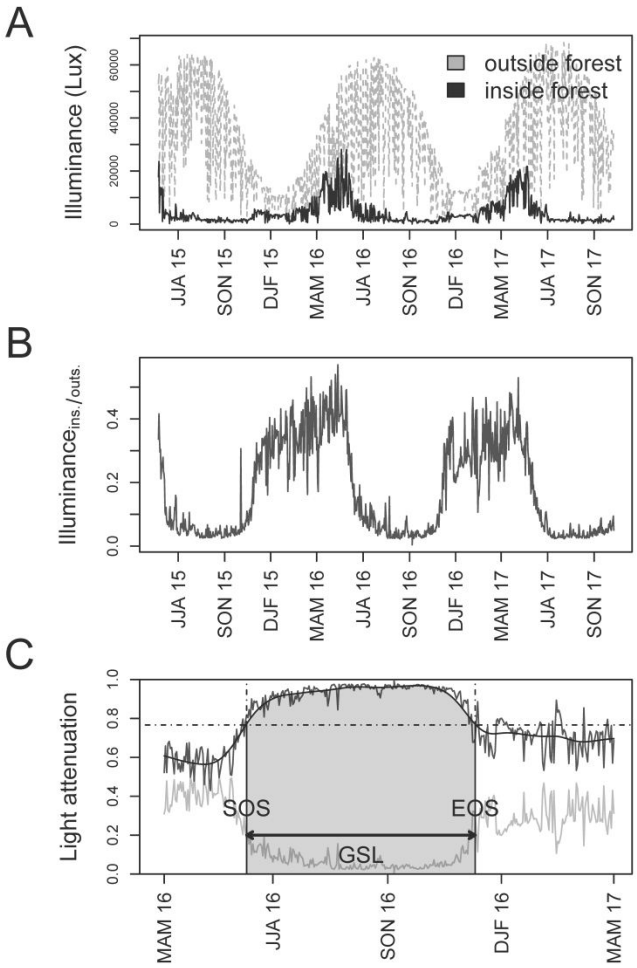


Fig. S1. **Overview of the light data processing derived from the light sensors we installed and maintained at the forest study sites. A**: Temporal development of average daily light (Lux) measured inside (dark grey) and outside (light grey) forest stands using corresponding sensors (HOBO UA-002-64; Onset Computer Corporation, Bourne, MA) in the time of spring 2015 (march, april, may; MAM) until autumn/winter 2017 (september, october, november; SON). **B:** Ratio of average daily (i.e. between 11.00 am and 4.00 pm) inside and outside illuminances as well as **C:** light attenuation by the forest canopy that we derived from the smoothed ratio of average daily inside and outside illuminances subtracted from 1. We defined yearly start of the season (SOS) as the day of the year where light attenuation first exceeded the mean of its annual minimum and maximum value and yearly end of the season (EOS) as the last day of year before light attenuation fell below this threshold. We then calculated yearly growing season length (GSL) as the number of days between SOS and EOS and finally averaged GSL for the years 2015 and 2016. We derived these metrics only for forests with a clear seasonal pattern in light attenuation, which we determined by applying the following restrictions: A minimum GSL of 60 days, a minimum growing season amplitude (i.e. 0.045) and a maximum number of detected periods of consecutive days above the mean of annual minimum and maximum light attenuation (i.e. 2) with a maximum number of days in between these periods (i.e. 8). In total, we obtained GSL values for a subset of 22 out of the 36 forest sites.

Fig. S2

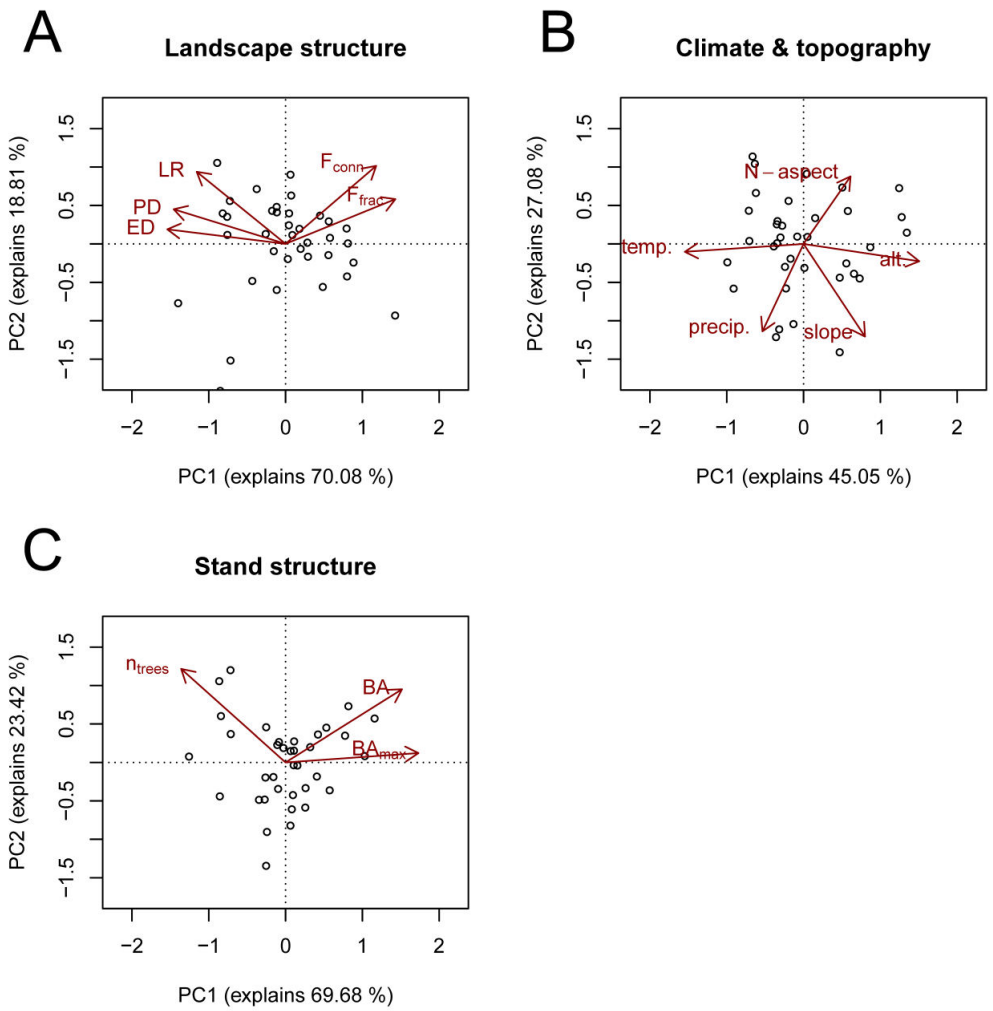
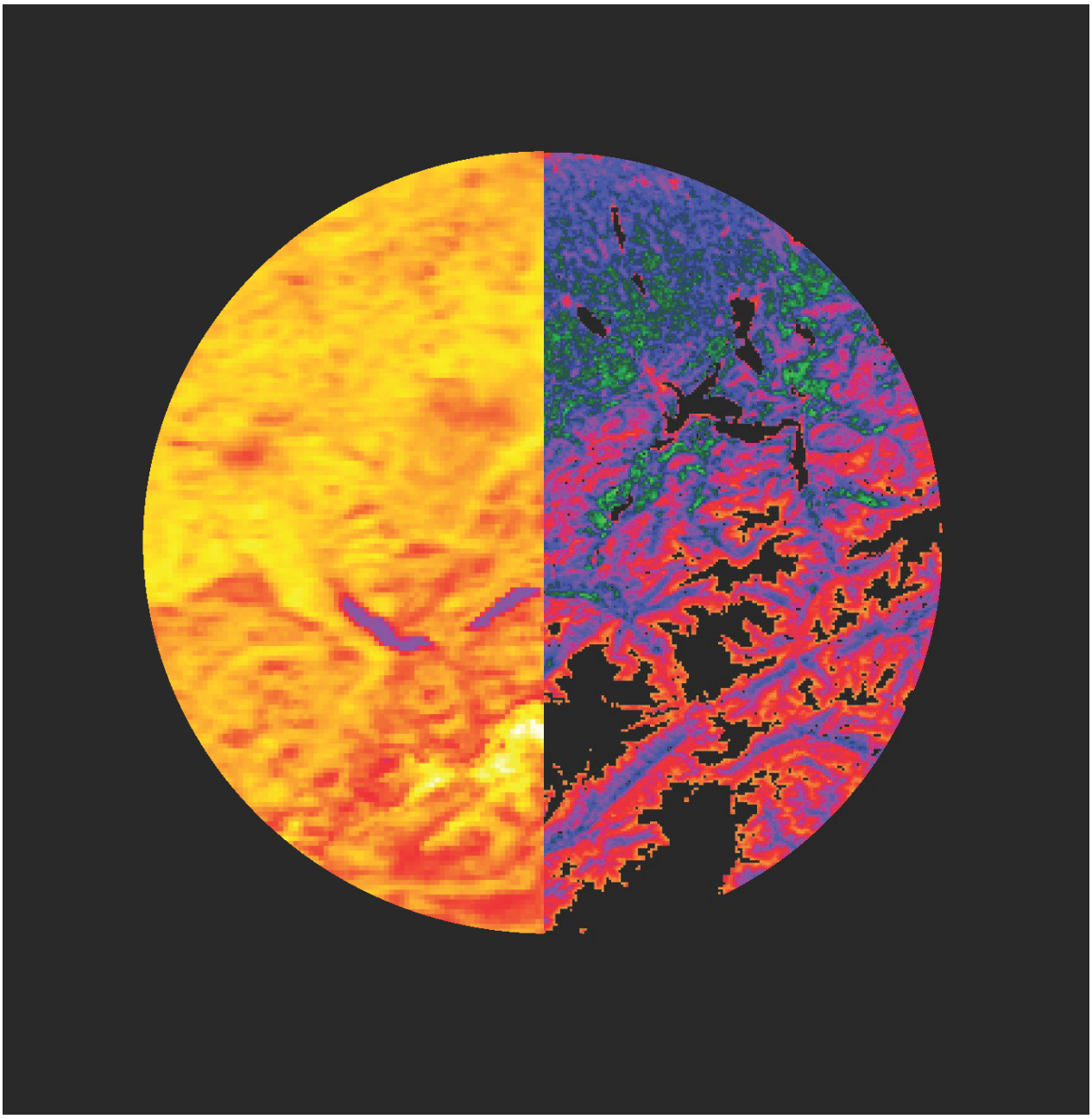


Fig. S2. **Principal component analyses (PCA) of variables related to landscape structure (A), climate and topography (B), and local stand structure (C). A:** Edge density (ED; total length of borders between two different land-cover types divided by the total landscape area), patch density (PD; the number of different land-cover patches divided by the total area of the landscape) and land-cover richness (LR; the number of different land-cover types) closely clustered together and strongly differed in their loadings compared to the fraction of forest cover (F_{frac}) and the connectivity of forest patches (F_{conn}) for the first principal component (PC1). **B:** Temperature (temp.) and altitude (alt.) showed the strongest negative covariance in loadings for PC1, indicating a strong temperature-altitude gradient in our dataset. We identified a second important gradient defined by precipitation (precip.) that positively co-varied with slope and negatively co-varied with the northerly aspect (N-aspect) in their loadings for the second principal component (PC2). **C:** Our proxy for stand age and demographic structure BA_{max} (average basal area of the three largest trees) clustered closely with cumulative basal area (BA) and both of these measures co-varied negatively with the number of trees (n_{trees}) in their loadings for PC1.

Chapter 2: Landscape diversity promotes landscape-level functioning



Land-surface albedo (left) and primary productivity (right) in a satellite's perspective

Landscape diversity promotes landscape-level functioning

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Abstract

More than two decades of biodiversity–ecosystem functioning (BEF) research have shown that alpha (i.e. local) biodiversity is fundamental for ecosystem functioning and stability at small spatial scales. It is conceivable that at larger spatial scales, beta diversity between local biotic communities similarly contributes to ecosystem functioning and stability. To test this hypothesis, we investigated the effect of land-cover type richness as a proxy for beta diversity on landscape functioning related to carbon and energy fluxes derived from satellite-remote sensing. Our dataset included 3,862 “landscape plots” of 250×250 m area and 704 plots of 500×500 m area spanning large altitudinal and climatic gradients. Profiting from extensive amounts of available data, we selected these plots according to a quasi-experimental study design where land-cover type richness was balanced and orthogonal with respect to environmental conditions. Land-cover type richness showed positive relationships with landscape primary productivity and land-surface albedo and with their temporal stability over time of 2000-2016. These relationships were stronger for the larger plots but largely independent of climatic and topographic contexts. Our findings suggest that landscape diversity promotes landscape functioning. Increasing landscape diversity may be a new management approach to maintain landscape functioning in the face of environmental change, a much needed step for both economic and conservation reasons.

Keywords: Landscape resilience and sustainability, beta diversity and stability, ecosystem function and services; MODIS EVI NDVI land surface phenology and albedo; large spatial scale; non-experimental, real-world ecosystems; alpha beta gamma variability; meta-ecosystems; spatial asynchrony; landscape diversity; landscape functioning

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Statement of authorship:
BS, GS, JO and PAN conceived the study
JO and PAN collected, prepared and analyzed the data
JO and PAN wrote the first draft of the manuscript and all authors contributed to revisions

Introduction

A vast body of evidence supports the notion of positive biodiversity effects on ecosystem functioning (Tilman *et al.* 2014). This evidence mainly originates from studies in which plot-level species richness was manipulated experimentally and diversity effects were assessed for selected ecosystem functions, with productivity being the most prominent one. With few exceptions, the broad pattern is one of “positive decelerating” responses of productivity, i.e. productivity increases with species number but incremental benefits of additional species diminish with the number of species the system already contains (Tilman *et al.* 2014). A second important general trend is that species-rich systems buffer disturbances more effectively than species-poor systems, resulting in a higher temporal stability of ecosystem functioning (Tilman *et al.* 2014; Isbell *et al.* 2015). However, biodiversity–ecosystem functioning (BEF) studies to date have mostly focused on species-level diversity and relatively small experimental field plots (Balvanera *et al.* 2006). It therefore remains unclear to which extent these findings can be extrapolated to biodiversity effects in so called “real-world” systems (Srivastava & Vellend 2005; Duffy 2009; Wardle 2016). This appears critical in light of the enormous economic value of the services these systems provide to humans (Costanza *et al.* 2014), and given that diversity currently is lost globally at alarming rates, both at the species level (Pimm *et al.* 2014; Ceballos *et al.* 2015) and at larger scales by landscape homogenization (Vitousek *et al.* 1997; Western 2001; Baiser *et al.* 2012)

By today, about half of the global ecosystem production is appropriated to meet human needs (Vitousek *et al.* 1986; Foley *et al.* 2005). Most land surfaces have been turned into human-dominated landscape mosaics (Chapin *et al.* 2002; Ellis *et al.* 2010; Tscharntke *et al.* 2012). These can be viewed as heterogeneous patchworks of cultural and natural elements in which ecosystems are strongly interconnected by the exchange of energy, matter and organisms across the hydrosphere, biosphere, and atmosphere (Chapin *et al.* 2002; Loreau *et al.* 2003b; Heffernan *et al.* 2014; Walz 2015). In these “meta-ecosystems” (Loreau *et al.* 2003b), ecological patterns and processes act and interact at multiple scales of space, time and ecological organization, which can lead to novel, emergent and unexpected behaviors (Levin 1992; Heffernan *et al.* 2014).

Recent theoretical analyses suggest that not only local-scale α-diversity but also the spatial dissimilarities among biotic communities and ecosystems, i.e. β-diversity (Whittaker

1972), affect regional-scale functioning in meta-ecosystems (Wang & Loreau 2014; Wang & Loreau 2016), here referred to as landscape functioning. Specifically, β-diversity may stabilize landscape functioning via spatial insurance effects mediated by the pool of species dispersing in a landscape (Loreau *et al.* 2003a; Isbell *et al.* 2018), which critically depends on the potential regional niche differentiation and the habitat connectivity (Leibold *et al.* 2004; Mouquet *et al.* 2006) determined by the biotic and abiotic spatial heterogeneity of a landscape (Stein *et al.* 2014). Further stabilizing β-diversity effects may result from the mere spatial decorrelation of the environment including spatial asynchrony in community dynamics (Olden *et al.* 2004; Wang & Loreau 2016) and the spatial asynchrony in ecosystem-atmosphere interactions (Moran 1953) that both operate at ranges beyond the typical plot scale of traditional B-EF experiments. Spatial variability in vegetation characteristics and activity plays a central role because these modulate biogeochemical carbon and water fluxes as well as surface physical properties such as albedo and roughness length (Oke 2002; McPherson 2007), resulting in landscape-heterogeneity effects on landscape-level temperature, precipitation and wind shear patterns (Pielke 2001; Laurance *et al.* 2011). Heat island and oasis effects around urban areas also have been shown to affect ecosystem functioning and stability (Bonan 2008; Connors *et al.* 2013; Mahmood *et al.* 2014).

Because scaling-up plot-scale BEF relationships to real-world landscapes remains challenging, working with a focus on whole systems at larger scales may be a valuable alternative (Heffernan *et al.* 2014). In this study we apply such a large-scale systems perspective to test whether spatial dissimilarities among ecosystems or landscape elements, hereafter referred to as “landscape diversity” (LD), affect the functioning and stability of the corresponding meta-ecosystems, here referred to as landscapes. We used land-cover type richness as metric for LD and analyze its relationship with primary productivity, phenology, albedo and the temporal stability of these variables as measures of landscape functioning (LF). We further analyze whether these LDLF relationships change with environmental context and compare their magnitude to BEF relationships derived from experiments.

Metrics of primary productivity and albedo were derived from satellite-sensed data available at high spatio-temporal resolution (MODIS EVI and albedo products (Didan 2015; Schaaf & Wan 2015), years 2000–2016). A notorious challenge in observational studies is the correlation of multiple putative drivers which results in statistical confounding. To

maximize statistical power and minimize such uncertainties in inferred cause-effect relationships, we adopted design principles from experimental biodiversity research. We first subdivided our study area based on combinations of biogeographic regions and altitude ranges (Fig. 1A). The rationale for this blocking was that species sets and landscape management likely varied between these blocks, as would diversity-independent drivers of putative response variables. Within each block, we then selected landscapes that spanned LD-gradients that were orthogonal to land-cover composition; in other words, the average land cover type composition remained constant across LD levels (Table 1). The landscapes within a block were randomly selected, with the constraint that these needed to be well-spread in space, land-cover evenness needed to be high in mixed landscapes, and that altitude, slope and the north-south aspect were similarly distributed in all compositions of land-cover types. This procedure was repeated separately for landscape plots of 250×250 m and 500×500 m area, resulting in two independent, non-overlapping data sets encompassing 3,862 and 704 plots, respectively.

Results

Primary productivity and phenology

Growing season length (GSL; Methods; Fig. 1B), increased significantly with LD in 500x500 m landscapes ($P<0.05$; Fig. 2). This effect was driven by an earlier start of season (SOS) at high LD ($P<0.05$; Table S1) but unaltered end of season (EOS; n.s.; Table S1). No significant corresponding effect was found in the 250x250 m landscapes (Fig. 2; Table S1). Average growing-season productivity ($\overline{EVI}$; Methods; Fig. 1B) and integrated growing-season productivity (EVI_{GS}; Methods; Fig. 1B) increased with LD in both 250x250 m and 500x500 m landscapes (all $P<0.05$; Fig. 2; Table S1). LD effects were similar when considering annual peak EVI (EVI_{max}; $P<0.05$; Fig. 2; Table S1). Both 250x250 m and 500x500 m landscapes exhibited overyielding (OY; Methods), i.e. $\overline{EVI}$ and EVI_{GS} of mixed landscapes (LD>1) exceeded the average of single land-cover landscapes (LD=1) with the land covers they contained; this overyielding effect was larger at higher LD ($P<0.05$; Fig. 3; see Table S1 for coefficient estimates and F-values).

Land surface albedo

LD was unrelated to summer land-surface albedo in the three spectral ranges (α_{SW}, α_{NIR}, α_{VIS}; Methods; Table S1). However, α_{NIR} but not α_{SW} and α_{VIS} overyielded, and this effect increased with LD (Fig.3; Table S1).

Temporal stability

We quantified stability as the inverse inter-annual coefficient of variation of the respective dependent variables (CV^{-1}; years 2000–2016). In 500x500 m landscapes, the stability of growing season length ($\mathrm{CV}_{\mathrm{GSL}}^{-1}$) increased with LD (P<0.05; Fig. 4A; Table S1). Similar effects were found for the stability of average growing-season productivity ($\mathrm{CV}_{\overline{\mathrm{EVI}}}^{-1}$) and integrated growing-season productivity ($\mathrm{CV}_{\mathrm{EVI_{GS}}}^{-1}$) and maximum growing-season productivity ($\mathrm{CV}_{\mathrm{EVI_{max}}}^{-1}$; P<0.05; Fig. 4A; Table S1). We found the same but weaker patterns in the smaller 250x250 m landscapes where effects were significant for $\mathrm{CV}_{\overline{\mathrm{EVI}}}^{-1}$ (P<0.05; Fig.4A) and $\mathrm{CV}_{\mathrm{EVI_{max}}}^{-1}$(P<0.05; Table S1), as well as marginally significant for $\mathrm{CV}_{\mathrm{GSL}}^{-1}$ (P<0.1; Fig.4A).

The inter-annual stability of summer land surface albedo (June—August) increased with LD in the near-infrared ($\mathrm{CV}_{\alpha_{\mathrm{NIR}}}^{-1}$; P<0.05; Fig. 4B) but not in the visible ($\mathrm{CV}_{\alpha_{\mathrm{vis}}}^{-1}$) or total short-wave range ($\mathrm{CV}_{\alpha_{\mathrm{SW}}}^{-1}$).

Context-dependence

While the investigated landscape functioning metrics depended on biogeographic region (BGR) and altitude range (ALT), all observed LD effects were independent of altitude and biogeographic region (LD×BGR: n.s.; LD×ALT: n.s.). However, we found evidence of long-range interactions of land-cover types. For example, the fractional cover of water surrounding ”forest monoculture” landscapes (W_{frac}, within a 500 m and a 1000 m radius from the center of 250x250 m and 500x500 m landscapes, respectively) was negatively related to average growing-season productivity ($\overline{\mathrm{EVI}}$; $F_{1,163}$=23, P<0.001 in 250x250 m landscapes and $F_{1,18}$=3, P<0. 1 in 500x500 m landscapes; Figs. S1 A, B). Conversely, the surrounding fractional cover of agricultural area (A_{frac}) was positively related to growing season length (GSL) in 250x250 m landscapes ($F_{1,163}$=14: P<0.001), but not in 500x500 landscapes ($F_{1,18}$=0: P=n.s.; Fig.S1C). However, we found no indication of the

dependence of LD effects on the surrounding water or agricultural cover, if we included these variables in our models (LD× $W_{fraction}$: n.s.; LD× $A_{fraction}$: n.s.).

Scale dependence

The broad patterns we found were similar in 250x250 m and 500x500 m landscapes. However, some LD effects were significantly stronger in the larger than in the smaller landscapes. This was the case for growing season length (GSL; LD×scale: $F_{1,688}$=5: P<0.05; Fig.2), and this effect was mediated by a change in SOS but not EOS (LD×scale: $F_{1,76}$=6: P<0.05 for SOS; n.s. for EOS). A similar effect was found for overyielding of GSL (OY_{GSL}; LD×scale: $F_{1,525}$=5: P<0.05; Fig.3), the stability of GSL (CV_{GSL}^{-1}; LD×scale: $F_{1,312}$=5: P<0.05; Fig.4A), the stability of average growing-season productivity ($CV_{\overline{EVI}}^{-1}$; LD×scale: $F_{1,143}$=12: P<0.001; Fig.4A) and the stability of maximum growing season productivity ($CV_{EVI_{max}}^{-1}$; LD×scale: $F_{1,691}$=6: P<0.05).

Relative importance of landscape diversity

We quantified the relative importance of LD for all the dependent variables (listed in Table S2) by calculating normalized effect sizes (Z_r; Fisher's z-transformation based on correlation coefficients derived from F-ratios; (Rosenthal 1994); Fig.5). Significant values of Z_r ranged between ~0.12-0.44 and were always larger in 500x500 m than in 250x250 m landscapes. These Z_r coefficients are slightly smaller than average Zr values derived from small-scale grassland experiments (Methods; Z_r=0.33 and 0.53 for effects on productivity and temporal stability of productivity, respectively).

Discussion

Our study adopted design principles from experimental biodiversity research to test whether landscape diversity, quantified here as land-cover type richness of meta-ecosystems, was related to landscape functioning in the "real-world" context (Duffy 2009). Using a 17-year time series encompassing 4,566 "landscape plots" deliberately selected to represent orthogonal and balanced richness gradients of land-cover types from 1–6 with even abundance in mixture, we demonstrate a linear increase in landscape functioning

(LF) with landscape diversity (LD). The affected variables measuring landscape functioning were primary productivity, growing season length, near-infrared albedo and the temporal stability of these variables. These positive LDLF relationships were robust across broad ranges of environmental conditions defined by altitude and biogeographic region. Consistent with theory for biodiversity–ecosystem functioning (BEF) relationships (Isbell *et al.* 2018), the positive LDLF relationships tended to increase with the area of landscape plots from 6.25 ha to 25 ha.

Our analyses empirically support theoretical investigations which suggest that regional-scale stability (γ-stability, stability at the level of our landscape plots) might be promoted by both local α-diversity and the turnover of species across ecosystems, i.e. β-diversity, (Wang & Loreau 2014; Wang & Loreau 2016). The main mechanisms posited to support these effects are desynchronized population dynamics at the species (Yachi & Loreau 1999; Loreau *et al.* 2003a; Isbell *et al.* 2018) or the whole-community (Wang & Loreau 2016) level. To date, these concepts and their consequences remain poorly tested outside modeling contexts (but see Isbell *et al.* 2018). Notable exceptions are a study of sockeye salmon yields that were stabilized at the meta-population level due to low inter-population correlations in yield (Schindler *et al.* 2010), and a study of grassland plots that showed that asynchrony among plots within several study sites led to a stabilization of yield at the site level (Wilcox 2017). In both studies, the asynchrony among local species populations (Schindler et al.) and communities (Wilcox et al.) may have been caused by environmental heterogeneity and demographic stochasticity. Our study suggests that similar relations apply not only within but also across ecosystem types, at large scales of space.

Therefore, the observed positive landscape diversity (i.e. β-diversity) effects on the temporal stability of primary productivity, growing season length and near-infrared albedo in our study may have been caused by positive effects of mixing land-cover types on landscape-scale species diversity (γ-diversity; (Stein *et al.* 2014) and consequent spatial insurance effects (Loreau *et al.* 2003a) or consequent increases in local species diversity (α-diversity) and corresponding well-known mechanisms derived from small-scale BEF experiments (Yachi & Loreau 1999; Tilman *et al.* 2014). However, landscape diversity effects on landscape stability may also have been mediated via mechanisms independent of species diversity such as the mere spatial decorrelation of the environment (Wang & Loreau 2016) or by complementary exchanges of energy and matter (Loreau *et al.* 2003b;

Polis *et al.* 2004; Alsterberg *et al.* 2017) including micro-climatic effects (Pielke 2001; Laurance *et al.* 2011). In the following, we consider these possibilities separately.

No species inventories were available for our study landscapes to investigate if landscape diversity (LD; i.e. β-diversity) effects were mediated indirectly via α- or γ-diversity. To tentatively explore the relationship between LD and α- and γ-diversity, respectively, we used data from a national biodiversity monitoring initiative (biodiversitymonitoring.ch; Weber *et al.* 2004). The available data set of 447 regularly-spaced plots (each 1 km^2 in area; cf. Oehri *et al.* 2017) fully matched our study area (Switzerland) and nearly matched the study period (2000-2015 vs. 2000—2016). We calculated Pearson's product moment correlations for LD and γ-diversity of vascular plants as well as α-diversity (woody and non-woody species diversity approximating α-diversity in forests and meadows) for all 1 km^2 landscapes in blocks of BGR and altitude range matching our study design and finally averaged these correlations to one value. In all three cases LD and species diversity were positively, but not very strongly correlated (Pearson's product moment correlation of LD and plant γ-diversity: r=0.17±0.40; Pearson's correlation of LD and woody plants α-diversity: r=0.05±0.34 and correlation of LD and non-woody plants α-diversity: r=0.18±0.42). We therefore consider it unlikely that the observed LD effects were exclusively mediated via α-diversity or γ-diversity. Additionally, α-diversity and γ-diversity have often been found to peak at intermediate environmental heterogeneity because these conditions allow for "species sorting" across communities while enhancing local diversity through intermediate dispersal of species into suboptimal environments in which they would not persist otherwise ("mass-effect"; Leibold *et al.* 2004; Mouquet *et al.* 2006; Redon *et al.* 2014; Thompson & Gonzalez 2016). Similar unimodal relationships are expected based on habitat area – heterogeneity trade-offs (Allouche *et al.* 2012) with too high a heterogeneity decreasing habitat size and enhancing stochastic species extinctions. Regardless of the specific mechanisms, we never detected any unimodal or significantly non-linear LD-effects that would have suggested a peak functioning at intermediate LD.

To investigate the role of direct interactions among land-cover types not necessarily mediated via α- or γ-diversity, we analyzed the overyielding (Loreau 1998; Tilman 1999; Schmid *et al.* 2008) of mixed landscapes. Interestingly, overyielding of productivity, growing season length and near-infrared albedo strongly increased with higher levels of

LD, suggesting that mechanisms among different land-cover types increase landscape-level functioning similarly as mechanisms among species increase local-level functioning. However, overyielding increased linearly with LD and was not as pronounced at low levels of LD compared to higher levels of LD, which contrasts with findings from BEF experiments (Tilman *et al.* 2014). Because we could not break down the satellite-derived, landscape-level functions to contributions of single land-cover types within landscapes, we could not infer complementarity or selection effects using the additive partitioning scheme proposed by (Loreau & Hector 2001), as it is often done in BEF experiments. To nevertheless investigate the possibility of complementarity effects among land-cover types we assessed if there were specific pairwise combinations of land-cover types typically over- or underyielding by using mechanistic diallel analysis (Griffing 1956); SI Methods). This analysis allowed the partitioning of the functioning of landscapes with two land-cover types into additive average contributions of each individual land-cover type (GCA: “general combining abilities”) and deviations from these additive predictions (SCA: “specific combining abilities”). In this approach, the sum of GCAs represents the expected landscape functioning (LF), whereas the SCA measures the deviation from expected LF, which can be attributed to synergistic or antagonistic interactions among land-cover types similar to the measure of the average proportional deviation from expected yield ($\overline{D}$; (Loreau 1998) or the deviation from the total expected yield in mixture (ΔY) as it is defined by (Loreau & Hector 2001). This diallel analysis revealed predominantly positive GCA’s for all land-cover types and very small SCA’s for all land-cover type combinations, which means firstly that mixed landscapes with two land-cover types generally do not differ from landscapes with only a single land-cover type and secondly that there are no two land-cover type combinations typically exhibiting higher or lower LF levels as would be expected by measures of respective LF in “monocultures” (SI Results; Fig. S2).

These findings confirm the pattern of positive linear LD effects on LF via overyielding that only manifest at LD levels >2. Hence, LDLF relationships differ from typical BEF relationships found in biodiversity experiments, which generally show decelerating differences with increasing species diversity levels and largest biodiversity effects between monocultures and two-species mixtures (Balvanera *et al.* 2006; Tilman *et al.* 2014).

We can think of three different but not exclusive mechanisms that may explain this pattern. The first possibility is related to the simultaneous action of multiple processes.

BEF relationships have been shown to saturate more slowly when multiple ecosystem functions (Hector & Bagchi 2007) or the diversity of multiple taxa (Duffy *et al.* 2007) are considered simultaneously. Landscapes integrate a wider range of scales than small experimental plots, and thus also a larger set of ecological mechanisms that potentially support diversity effects. It can be argued, in analogy to effects of multi-functionality or multi-diversity, that these mechanisms likely differ in their scale properties and that therefore their combination will transform functioning responses from saturating to a more linear shape. The second possibility is that effects of land-cover type richness are mediated by higher-order interactions involving more than two land-cover types. Such higher-order interactions occur for example between species, where they lead to emergent patterns that potentially modify the productivity and stability of diverse communities (Levine *et al.* 2017). Finally, synergistic or antagonistic interactions between two specific species could be the result of co-evolution or similar processes that conceivably cannot be extrapolated to the landscape scale.

Hence, positive LD effects on landscape functions and stability likely are mediated by mechanisms dominantly emerging at higher levels of LD. In virtually all real-world landscapes, compositional diversity intrinsically is linked to configurational diversity. In other words, landscapes that differ in number of spatial landscape element identities per unit area also differ with respect to size, shape and arrangement of these elements (Duelli 1997; Fahrig *et al.* 2011; Pasher *et al.* 2013). We focused on the richness of land-cover types as a proxy of spatial dissimilarity of biotic communities in a landscape, in analogy to the species number as a proxy of functional trait dissimilarity in biodiversity experiments. However, there is no doubt that the spatial structure of land-cover types also is important. In our study, richness of land-cover types was highly correlated with measures of configurational diversity (SI Methods; SI Results; Table S3; Fig.S3). For example, edge density (the total length of borders between two different land-cover types) explained variance in productivity and phenology that was not explained by LD alone.

Interestingly, LD did not only affect function and stability of momentary vegetation activity ($\overline{\mathrm{EVI}}$; primarily 250x250 m landscapes) and growing-season length (GSL; primarily mediated via the start of season (SOS) in 500x500 m landscapes), but also increased the overyielding and stability of near-infrared albedo (α_{NIR}). The surface reflectance in the near-infrared domain lies at the heart of the EVI determination (Huete *et al.* 2002), raising

the possibility that these measure identical phenomena. However, redundancy analysis (RDA) showed that EVI and α_{NIR} reflect different and well separable properties of the land surface (Fig. S4), even though they are correlated ($\overline{\mathrm{EVI}}$~α_{NIR}: r=0.77; CV_{EVI}^{-1}~$CV_{\alpha_{NIR}}^{-1}$: r=0.76; SI Methods; SI Results; Fig.S5). Overall, this underlines that a more temporally stable productivity also implies a more constant biophysical climate forcing (Claussen *et al.* 2001; Oke 2002). Recent climate model analyses suggest that such CO_2-independent impacts on radiation budgets are important to mitigate climate change effects (Bright *et al.* 2015; Devaraju *et al.* 2015; Zeng *et al.* 2017). We found evidence for the importance of such effects on biophysical climate forcing for landscape functions in our datasets: For example, forested landscapes had a longer growing season when a larger fraction of agricultural land was present in their surroundings whereas, conversely, forest primary productivity decreased with the fraction of surrounding water (Fig.S1). These effects could be explained by spatial subsidies of nutrients (Polis *et al.* 2004) or by modifications of a shared surface energy budget between focal landscape and surrounding and highlight the potential importance of ecosystem-atmosphere interactions at large spatial scales (Bonan 2008; Connors *et al.* 2013; Mahmood *et al.* 2014). These findings highlight that landscape diversity affects a variety of landscape functions hitherto underexplored in BEF experiments, such as vegetation phenology and biogeophysical surface properties that are important for climate regulation.

It has previously been established that local biodiversity matters for local ecosystem functioning and stability. We now add empirical evidence and corroborate hypotheses from modeling analyses that, similarly, landscape diversity matters for landscape functioning. Considering landscapes as meta-ecosystems, this suggests that BEF relationships within ecosystems can be extrapolated to LDLF relationships among ecosystems and indicates a generality of diversity–functioning relationship in nature, which can also be found when extrapolating effects of within-species to between-species diversity (Paschke *et al.* 2002; Crutsinger *et al.* 2008; Wuest & Niklaus 2018). Some of the effects that we found at the landscape level appear to depend at least partially on emergent mechanisms independent of species diversity. We contend that landscape-level diversity–functioning effects deserve increased attention, not at least because they concern policy-relevant scales at which land development and management actions take place and which likely have consequences for ecosystem services delivered to humans. The use of quasi-experimental study designs

allowing for systematic investigations in real-world conditions demonstrates a valuable approach to tackle this challenge.

Methods

Study design

We established two networks of plots that contained landscapes with either a spatial extent of 250 × 250 m or 500 × 500 m; their boundaries were congruent with MODIS 250-m and 500-m Vegetation Index pixels (Didan 2015), respectively. The plot networks covered the entire area of Switzerland (41,248 km^2) and spanned an altitudinal range of 193 to 3,000 m above sea level (a.s.l). To account for regional variation in environmental conditions, we divided the study area into six biogeographic regions (BGR) that form distinct units with respect to climate, edaphic conditions and distribution patterns of fauna and flora (Wohlgemuth 1996). We then subdivided the six BGRs by altitude, using 500 m increments (Fig.1A). Not all land-cover (LC) types and type combinations occurred in the 36 established BGR x altitude blocks (Table 1). We therefore used a nested design with independent gradients in landscape diversity (LD; i.e. LC type richness) in each of these BGR x altitude blocks. Within each block, we determined the largest set of LC types that still allowed spanning a wide gradient in LD with all possible LC combinations realized. Hence, LD gradient and average LC abundance were orthogonal (Table 1). Using an optimization procedure, we then selected 12 replicates for each LC composition (LCC), with LCCs having a minimum evenness of component LCs ($1/D > 1.43$, D = Simpson's index of dominance). We further (1) maximized the minimum pairwise distance among all landscapes within a block, ensured (2) that landscapes of identical LCC were at least 1 km apart, (3) that the mean altitude, slope, and north-south aspect were as equally distributed as possible in all LCCs, and (4) that these values showed as little correlation as possible with LD. If not enough plots could be found that satisfied this criterion, we lowered the number of replicates per LCC in this particular block. The final plot set encompassed 3,862 and 704 landscapes of 250 m and 500 m extent, respectively (Table 1).

Landscape diversity

Landscape diversity (LD) was determined as the number of LC types found in a landscape. LC information was taken from 100-m spatial resolution point data available from the Swiss Federal Statistical Office (GEOSTAT, product name: NOAS04). The originally 17 LC types available were aggregated to the 8 classes, i.e. forest, grassland, arable, urban, urban green, water, unproductive and bare land (Fig. 1A), and their fractional land cover determined by clipping LC pixels at the boundaries of the study landscapes defined by the MODIS Vegetation Index pixels.

Primary productivity and phenology

We used space-borne MODIS Vegetation Index data (MOD13Q1 and MOD13A1; Didan 2015) with 250 m and 500 m spatial resolution and 16 days temporal resolution to derive land-surface phenology and growing season productivity metrics. Specifically, we used the enhanced vegetation index (EVI) which quantifies photosynthetically active vegetation from the ratio of reflected red and near-infrared light; it is similar to the normalized difference vegetation index (NDVI) but more robust (Huete *et al.* 2002). We derived the vegetation growing season for every study landscape and year from 2000 to 2016 using the $NDVI_{ratio}$ method (White *et al.* 1997), which defines the growing season as the time of the year when vegetation activity exceeds the mean of its annual minimum and maximum value (Fig. 1B; as described in Oehri *et al.* 2017). Growing seasons where thereby characterized by their start (SOS), end (EOS), and length (GSL). We used two primary productivity metrics; the first, $\overline{\mathrm{EVI}}$, equals the average growing season EVI. The second integrates EVI over the growing season: $EVI_{GS}=\int_{SOS}^{EOS} EVI(t)dt = \overline{\mathrm{EVI}}\,(EOS - SOS)$. We further determined peak growing season productivity (EVI_{max}).

Land surface albedo

We used space-borne land surface albedo (α) data (MODIS MCD43A3; Schaaf & Wan 2015) with a spatial resolution of 500 m. These data are created using multi-date (16 days), multi-band, cloud free, atmospherically corrected surface reflectance to derive white-sky (WSA) and black-sky (BSA) surface albedo. We used WSA because it is a property of the land surface itself, independent of the state of the atmosphere, and is used as input to climate models (Strahler A.H. *et al.* 1999). Specifically, we used the 17-year

average of mean yearly summer (June to August) shortwave WSA (α_{SW}: wavelengths 0.3–5.0 µm) and the respective averages of the yearly means of its two components near-infrared WSA (α_{NIR}: wavelengths 0.7–5.0 µm) and visible WSA (α_{vis}: wavelengths 0.3–0.7 µm) in this time. The partitioning of α_{SW} into α_{NIR} and α_{VIS} is important because of the marked difference of vegetation reflectance in these spectral domains (Lucht *et al.* 2000) and it has been found that climate models are more accurate when they incorporate this albedo variation within the shortwave spectrum (Roesch *et al.* 2002).

Stability

We quantified stability of all productivity and albedo metrics as inverse coefficients of variation (CV^{-1}) of their inter-annual variability (years 2000—2016, n=17).

Overyielding

Overyielding (OY) was calculated as the observed value of a metric in a mixed landscape (LD>1) minus its expected value. The expected value was the average metric of all single LC-type landscapes (LD=1) with a LC that occurred in the mixture. These calculations were done within the same block, i.e. BGR × altitude range combination. OY quantifies the change in a metric with an increase in LD, while adjusting for land-cover composition.

Statistical analysis

We tested effects of LD using general linear mixed models summarized by analysis of variance (ANOVA; ASReml-R package; VSN International, Hemel Hemsted, UK; R 3.3 ;http://r-project.org). Fixed effects were, in this order, BGR, ALT, BGR × ALT (the terms so far are equivalent to block) and LD. Because LC types strongly differed in their characteristic values of dependent variables (Fig. S6) it was important to add a term capturing this systematic difference. Therefore, we added the “fraction of low productivity LC types in each land-cover composition” (fracL; i.e. water, bare land, urban and unproductive vegetation) after the LD term in all models. Land-cover composition (LCC) was a random term defining the replication level for LD. Given the different LCCs in 250 m and 500 m landscapes, we analyzed these data sets separately, except to test for the scale dependence of effects in which case we included the fixed effects SCALE and

LD×SCALE plus the additional random effect LCC×SCALE. To test for the dependence of LD-effects on environmental context, we added LD×BGR and LD×ALT to the model, together with the matching random effects LCC×BGR and LCC×ALT. Similarly, we tested the dependence of LD-effects on the fraction of surrounding water (W_{frac}) or agricultural (A_{frac}) area (Fig. S1) by adding the fixed effects W_{frac} and LD×W_{frac} and the random effect LCC×W_{frac} to the models (analogously for A_{frac}). Prior to analysis, we aggregated all dependent variables to a single value for each block and land-cover composition (LCC), which reduced the number of study units from 3,862 “lanscape plots” to 504 unique LCC/block combinations in the case of the 250-m landscapes and from 704 landscape plots to 213 unique LCC/block combinations in the case of the 500-m landscapes. In this process, we also excluded extreme outliers that were more than 5.5 standard deviations from the mean. To compare effects on the different parameters, we determined normalized effect sizes (Z_r; Fisher’s z-transformation based on correlation coefficients derived from F-ratios; (Rosenthal 1994).

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Tables & Figures

Table 1. Study design for selected areas with different landscape extent (250 m and 500 m, respectively). We selected complete, balanced and randomized LD gradients in blocks (delineated with boxes) of BGR, ALT and landscape extent (250 m and 500 m) combinations. The specific land-cover type identities (brown: arable; dark-green: forest; purple: urban green; light-green: grass; yellow: unproductive; red: urban; grey: bare land; blue: water), as well as the number of landscape plots (p) and unique land-cover compositions (LCC) are shown for each block separately. The land-cover types, as well as corresponding p and LCC used in each BGR, ALT and landscape extent are shown in row- and column summary statistics without boxes ("All"). In total, we selected 3,862 landscape plots with areas of 250 m extent that formed 504 unique BGR/ALT/LCC combinations and 28 LD gradients ranging from 1-6 LC types. We selected analogously 704 landscape plots with areas of 500m extent that formed 213 unique BGR/ALT/LCC combinations and 23 LD gradients ranging from 1-5 LC types.

Landscape extent	Biogeographic region (BGR)	Altitude range (ALT; m)											
		0-500		500-1000		1000-1500		1500-2000		2000-2500		2500-3000		All	
		LC types	nr plots (p) LCC	LC types	nr plots (p) LCC	LC types	nr plots (p) LCC	LC types	nr plots (p) LCC	LC types	nr plots (p) LCC	LC types	nr plots (p) LCC	LC types	nr plots (p) LCC
250m	Northern Alps		p:362 LCC: 31		p:131 LCC:63		p:54 LCC:7		p:282 LCC:31		p:106 LCC:15	-	- -		p:935 LCC:147
	Southern Alps		p:55 LCC: 31		p: 16 LCC: 3		p:36 LCC:3		p:104 LCC:15		p:162 LCC15		p:22 LCC:3		p:395 LCC:70
	Jura Mountains		p:160 LCC: 15		p:180 LCC:15		p:64 LCC:15		p:28 LCC:3	-	- -	-	- -		p:432 LCC:48

	Central Plateau	p:666 LCC:63	p:357 LCC:63	-	-	-	-	p:1023 LCC126	
	Eastern Central Alps	-	p:112 LCC:15	p:63 LCC:7	p:120 LCC:15	p:180 LCC15	p:84 LCC:7	p:559 LCC:59	
	Western Central Alps	p:28 LCC:3	p:128 LCC:15	p:36 LCC:3	p:110 LCC:15	p:180 LCC:15	p:36 LCC:3	p:518 LCC:54	
	All	p:1271 LCC: 143	p:924 LCC:174	p:253 LCC:35	p:644 LCC:79	p:628 LCC:60	p:142 LCC:13	p:3862 LCC:504	
500m	Northern Alps	p:39 LCC:15	p:52 LCC:15	p:26 LCC:3	p:29 LCC:15	p:26 LCC:3	-	p:172 LCC:51	
	Southern Alps	p:20 LCC:7	p:3 LCC:3	-	p:19 LCC:7	p:6 LCC:3	-	p:48 LCC:20	
	Jura Mountains	p:24 LCC:7	p:30 LCC:7	p:12 LCC:7	p:4 LCC:3	-	-	p:70 LCC:24	
	Central Plateau	p:153 LCC:31	p:77 LCC:31	-	-	-	-	p:230 LCC:62	
	Eastern Central Alps	-	-	p:10 LCC:3	p:18 LCC:7	p:61 LCC:15	p:14 LCC:3	p:103 LCC:28	
	Western Central Alps	-	p:6 LCC:3	-	p:7 LCC:3	p:48 LCC:15	p:20 LCC:7	p:81 LCC:28	
	All	p:236 LCC:60	p:168 LCC:59	p:48 LCC:13	p:77 LCC:35	p:141 LCC:36	p:34 LCC:10	p:704 LCC:213	

Fig. 1

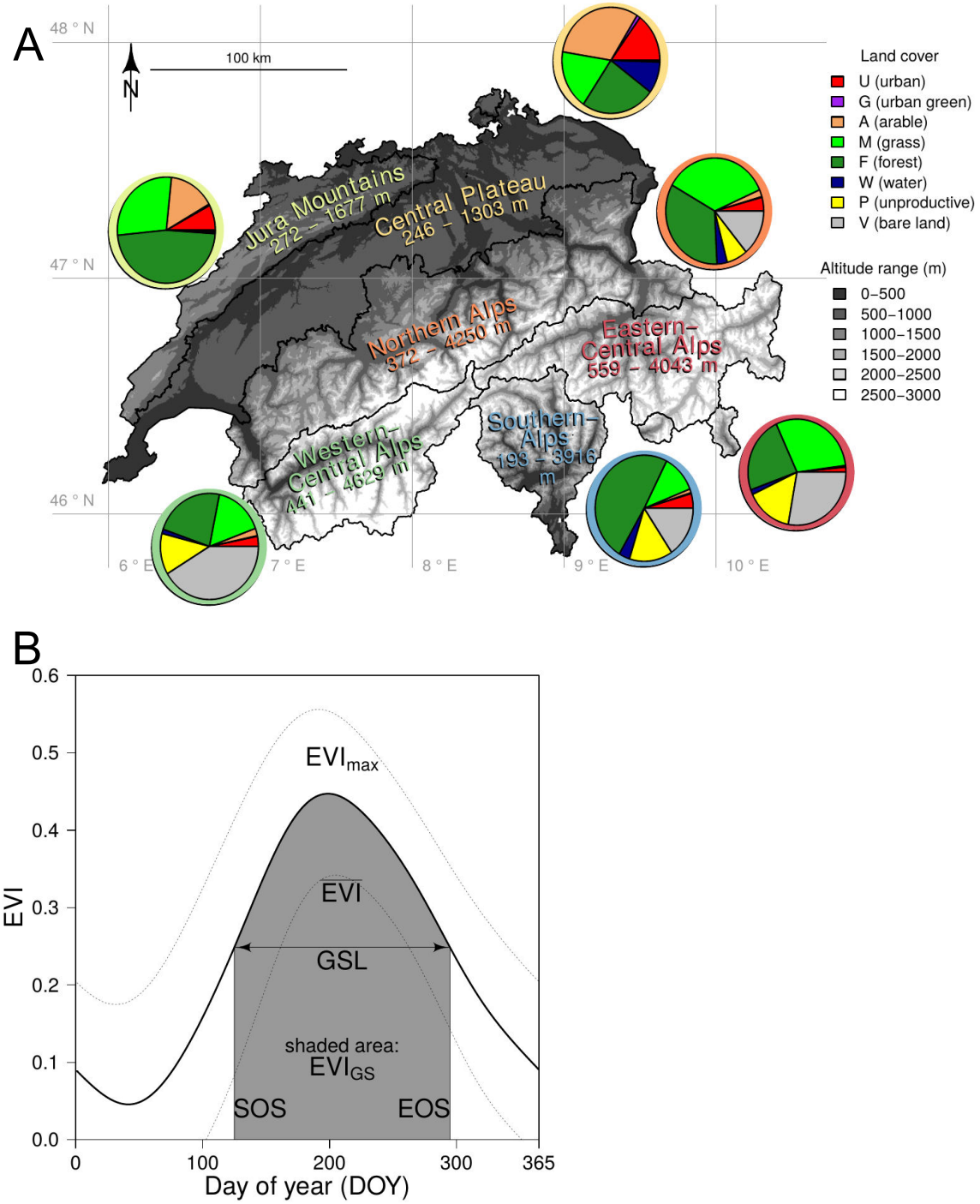

Fig. 1. **Study region (Switzerland, Central Europe; A) and phenometrics (B). A**: We selected complete and balanced land-cover richness (LD) gradients in blocks of BGR and altitude range (ALT; grey shades) combinations. **B**: We smoothed the EVI data (black line; see Methods for details) and derived phenometrics, i.e. growing season length (GSL); start (SOS) and end (EOS) of season; and primary productivity, i.e. average and maximum growing-season EVI ($\overline{EVI}$ and EVI_{max}) and the growing season integrated EVI (EVI_{GS}).

Fig. 2

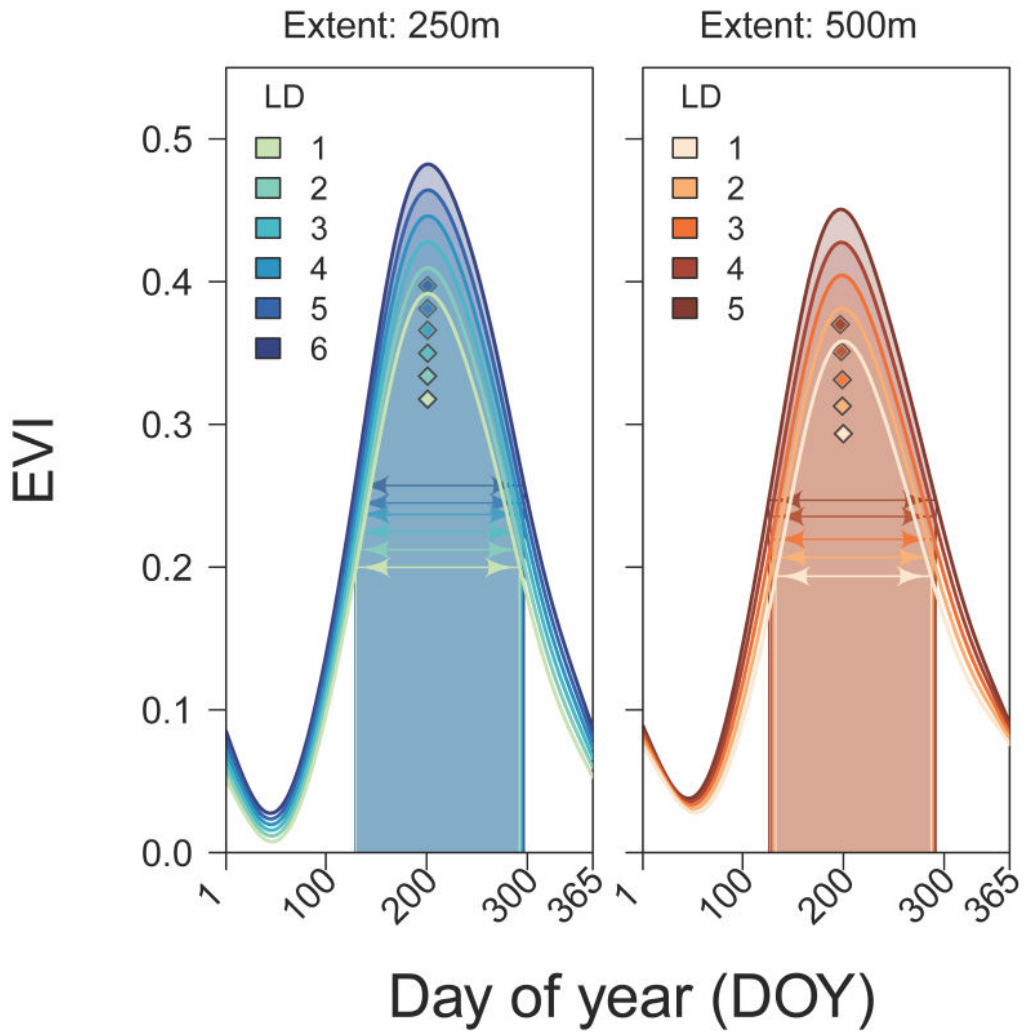

Fig. 2. **Landscape diversity (LD) effects on primary productivity ($\overline{EVI}$ and EVI_{GS}) and phenology (growing season length: GSL) proxies.** Mixed-effects model predictions of daily EVI values for different LD levels after accounting for effects of BGR, ALT and their interaction as fixed effects and the specific land-cover composition (LCC) as random effect in datasets spanning 17-year EVI time-series derived from landscapes with 250 m (n=504) or 500 m (n=213) extent. Proxies of primary productivity ($\overline{EVI}$ [dots] and EVI_{GS} [areas below curves]) increased with LD at both spatial scales ($P<0.05$; see Table S1 for F-values and coefficient estimates), whereas LD effects on a prolonged growing season length (GSL [arrows]) were only significant in landscapes of 500 m spatial extent (landscape extent of 250 m: $P>0.1$; landscape extent of 500 m: $P<0.05$; see Table S1).

Fig. 3

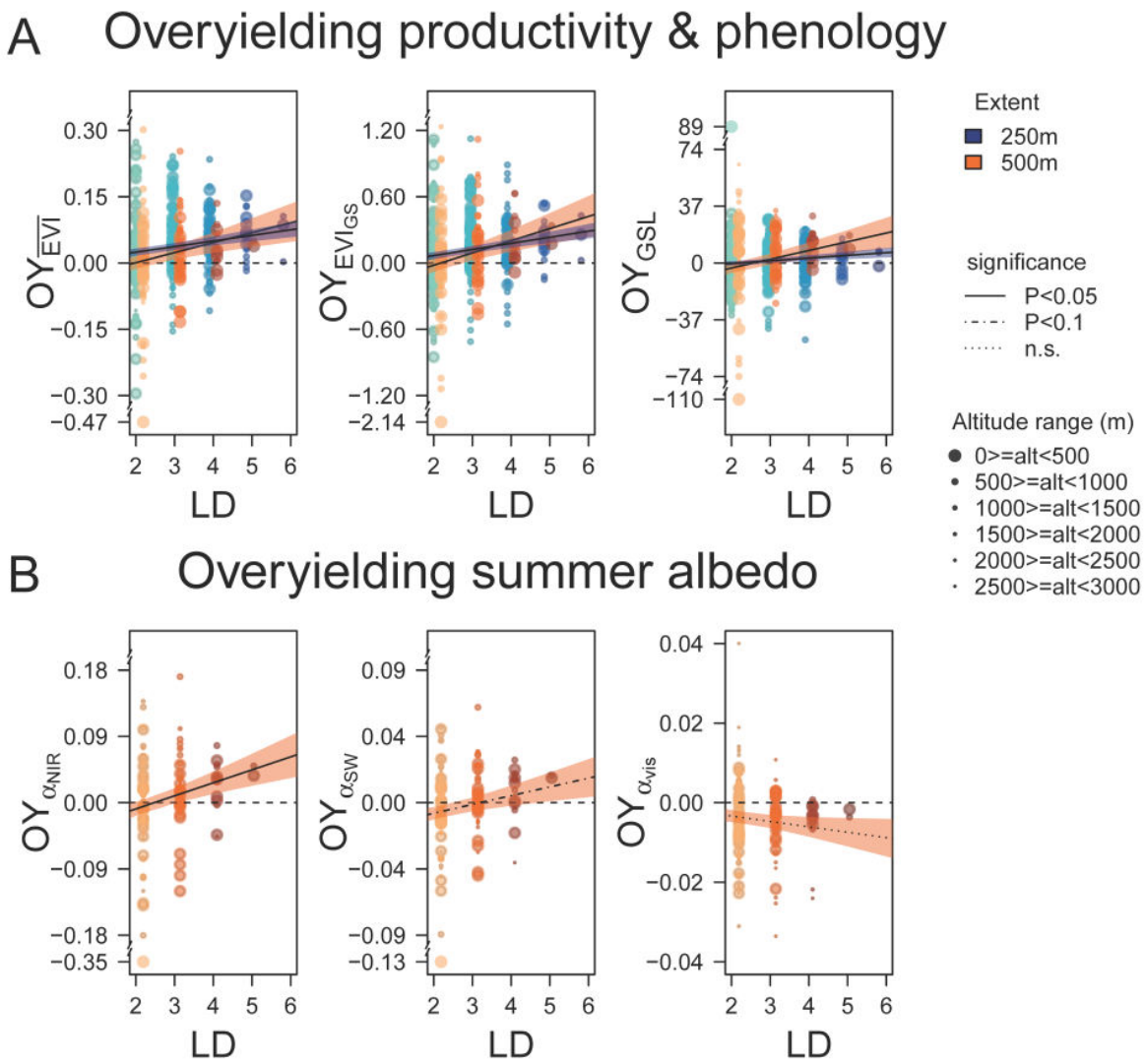

Fig. 3. **Overyielding (OY) of primary productivity and phenology proxies ($\overline{EVI}$, GSL EVI_{GS}), and summer albedo (α_{NIR}, α_{vis} and α_{SW}).** The overyielding (OY) (i.e. the absolute difference between observed values and expected values based on average single land-cover type values; see Methods) for primary productivity proxies ($\overline{EVI}$ and EVI_{GS}), as well as for growing season length (GSL) increased with LD in both landscape extents (P<0.05; see Table S1 for F-values and coefficient estimates). Also, summer (June-August) albedo in the near-infrared domain (α_{NIR}) showed a significant increase with LD (P<0.05), whereas summer albedo in the visible (α_{vis}) and shortwave (α_{SW}) domains were not significantly related to LD (P>0.05). Data points show average OY for every land-cover composition (LCC) in each BGR/ALT combination, and are sized according to their corresponding ALT. Lines show model predictions with associated standard error of the mean from different datasets (landscape extent of 250 m in blue; n=504; landscape extent of 500 m in orange; n=213) and significances are shown with line types.

Fig. 4

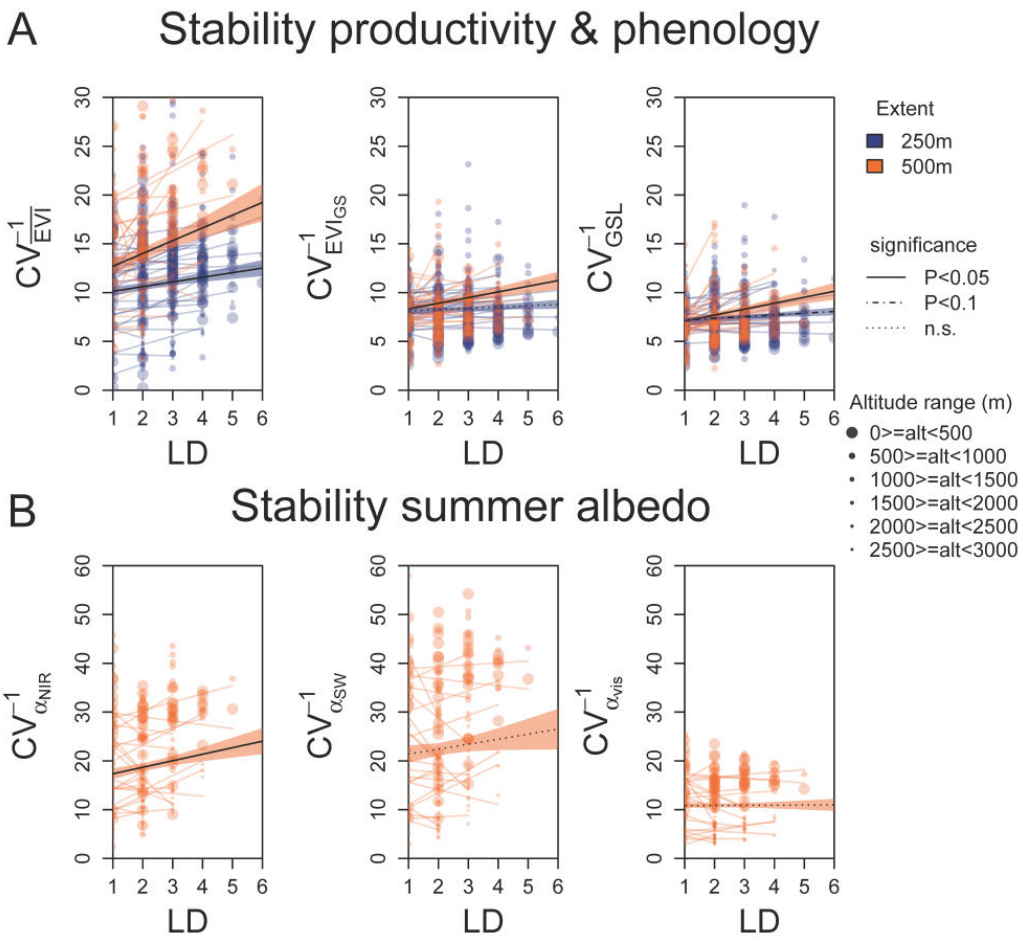

Fig. 4. **Landscape diversity (LD) effects on temporal stability of primary productivity and phenometrics (CV^{-1}_{EVI},CV^{-1}_{GSL},$CV^{-1}_{EVI_{GS}}$) (A), and summer albedo ($CV^{-1}_{\alpha_{SW}}$, $CV^{-1}_{\alpha_{nir}}$, $CV^{-1}_{\alpha_{vis}}$) (B).** Data points show average temporal stability for every land-cover composition (LCC) in each BGR/ALT combination, points are sized according to their corresponding ALT, and black lines show model predictions with associated standard error of the mean. Corresponding significances of model predictions are shown with line types. Model predictions for LD in different datasets in the BGR/ALT blocks are separately shown with thin lines in blue (landscape extent 250 m: n=504; Table 1) and in orange (landscape extent 500 m: n=213; Table 1). **A**: The temporal stability of the yearly average growing season EVI (CV^{-1}_{EVI}) strongly increased with LD in both datasets (P<0.05; Table S1). The yearly integrated EVI ($CV^{-1}_{EVI_{GS}}$) and the growing season length (CV^{-1}_{GSL}) strongly increased with LD in the 500m extent landscapes (P<0.01; Table S1), whereas increments in the 250m extent landscapes were not or only marginally significant, respectively (Table S1). **B**: The temporal stability of surface near-infrared albedo ($CV^{-1}_{\alpha_{NIR}}$) increased with LD (P<0.05), whereas $CV^{-1}_{\alpha_{SW}}$ and $CV^{-1}_{\alpha_{vis}}$ were unaffected by LD (P<0.1 and P: n.s.). See Table S1 for F-values and coefficient estimates.

Fig. 5

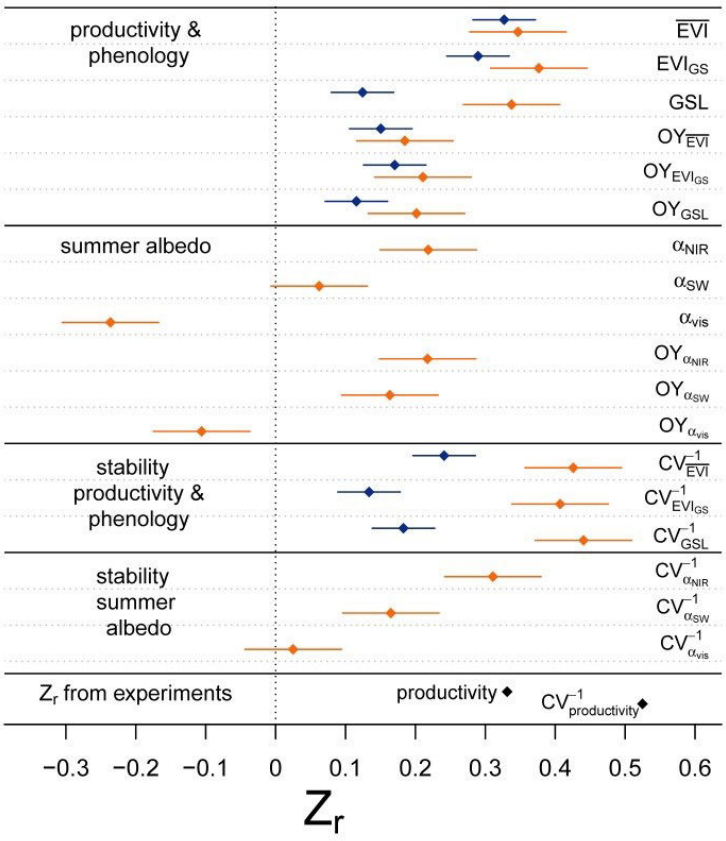

Fig. 5. **Magnitude of effects of landscape diversity (LD) on productivity and phenology proxies ($\overline{EVI}$, GSL, EVI_{GS}, $OY_{\overline{EVI}}$, OY_{GSL}, $OY_{EVI_{GS}}$), summer land surface albedo (α_{SW}, α_{NIR}, α_{vis}, $OY_{\alpha_{SW}}$, $OY_{\alpha_{NIR}}$, $OY_{\alpha_{vis}}$) and the temporal stability thereof (CV^{-1}) compared to biodiversity effects on productivity and its stability derived from experiments.** Shown are normalized effect sizes (Z_r) as used in meta-analysis (z-transformed, based on F-ratios) of LD derived from the two datasets containing landscapes of 250 m extent (blue; n=504) and 500 m extent (orange; n=213) as well as of biodiversity effects in small-scale grassland experiments. Zr of small-scale grassland experiments (black) are averages of already published Z_r values of plant diversity effects on plant community aboveground biomass in grassland field experiments (13 studies and 15 biodiversity effects from data published by (Balvanera *et al.* 2006) and accessible in Schmid *et al.* 2009) in the case of productivity and averages of Z_r values we derived from published F-ratios of three major field experiments (Tilman *et al.* 2006; van Ruijven & Berendse 2007; Roscher *et al.* 2011) in the case of the temporal stability of productivity. Table S2 lists a detailed description of the dependent variables shown on the right side of the graph, which belong to the broad categories shown on the left side of the graph. Error bars show standard errors of the mean. See Table S1 for F-values, significances and coefficient estimates.

SI Methods

Pairwise interactions of land-cover types

We investigated if pairwise interactions among land-cover types could qualify as potential mechanisms behind effects of landscape diversity. In order to achieve this, we used mechanistic diallel analysis (Griffing 1956), which was originally developed to model the performance of homo- and heterozygote crosses as a function of i) the general contributions and ii) the specific combination of the two parental alleles. This method can be used to investigate any orthogonal setting of units composed of one or two components, where units with one component correspond to the case where both parental alleles are identical. Diallel analysis composes the net difference in performance of units comprising one or two components, respectively, into "general combining abilities" (GCA) and "specific combining abilities" (SCA) by fitting the following model:

$$y_{a,b,i} \sim GCA_a + GCA_b + SCA_{a,b} + \varepsilon_{a,b,i} \quad (3)$$

Where $y_{a,b,i}$ represents the performance of the unit comprising component a and b (where $a = b$ in the case of identical components) in replicate i, GCA_n represents the average contribution of the component n to the general performance of units across the study, $SCA_{a,b}$ is the average contribution of the specific combination of components a and b and $\varepsilon_{a,b,i}$ is the corresponding residual.

While the sum of the GCA's is equal to the expected performance, the SCA's represent the deviation from this value and therefore serve as a measure for the net interaction of two specific components. This framework thus can be used to identify positive or negative interactions between two identical or different components of a unit, similar to the additive partitioning scheme proposed by Loreau and Hector (Loreau & Hector 2001), with the advantage that the performance of units with two components only needs to be measured at the whole-unit level and not at the individual component level.

In our study, we applied the mechanistic diallel analysis to the subset of our data where LD <=2, separately for every block of BGR/ALT combination that contained data. We calculated the GCA for a specific land-cover type in each BGR/ALT combination as the average landscape functioning of all LCC's (1 <= LD <= 2) containing this specific land-cover type. We calculated SCA as the difference between the observed value and the expected value based on the two constituent GCA values for every LCC in every BGR/ALT combination.

To this purpose, we constructed superimposed model matrices coding for the identity of the two different or identical land-cover types (i.e. GCA terms) that were combined in a specific LCC using the "and()" special function of ASReml (VSN International, Hemel Hemsted, UK). We estimated the significance of SCA by fitting the specific LCC identity as a fixed effect after the GCA terms. Since estimated coefficients for GCA and SCA were difficult to directly extract from the mixed model due to aliasing, we separately determined these using linear models where dependent variables were a function of the two respective GCA's without intercept (i.e. y~-1). SCA was calculated as the difference between the actual, observed values and predicted values based on the sum of the two respective GCA values. We calculated GCA's and SCA's for every BGR/ALT combination and 250 m and 500 m landscapes separately. Then, we averaged GCA and SCA values for each LCC across BGR/ALT combinations and tested if SCA values differed between landscapes of two identical land-cover types (i.e. LD=1) and landscapes of two different land-cover types (i.e. LD=2) by using linear models.

Landscape structural diversity

For each of the 250 m and 500 m study landscapes, we determined structural diversity of land-cover types (i.e. edge density (ED), effective mesh size (MESH), Simpson's diversity Index (SIDI), Simpson's evenness index (SIEI) and patch cohesion index (COHESION); Table S3; McGarigal 2015) from the aggregated land-cover point data (Methods section main text) using the ClassStat and PatchStat functions in the SDMTools package in R (https://cran.r-project.org/web/packages/SDMTools/index.html).

Subsequently, we determined their respective correlation with LD using Pearson's r. Then we assessed the bilateral statistical confounding of LD and structural diversity effects, by fitting structural diversity variables before and after LD in the model specified in the Methods section.

Interrelation of primary productivity, phenology and albedo proxies

Many of the dependent variables we tested are correlated by definition. This was the case for EVI_{GS}, which can be expressed as a function of $\overline{\mathrm{EVI}}$, SOS and EOS and consequently, GSL (see Methods section of the main text) and α_{SW}, which covers about the same range of electromagnetic wavelengths that is covered by α_{NIR} and α_{vis} together (Schaaf & Wan 2015). Furthermore, the reflection in the near-infrared spectrum lies at the

heart of the definition of EVI (Huete *et al.* 2002), and therefore EVI and α_{NIR} derived measures are inherently correlated with each other as well. We quantified the degree of correlation of these dependent variables for the 500 m landscapes by means of Pearson's product moment correlation. Furthermore, we used Redundancy analysis (RDA; https://cran.r-project.org/web/packages/vegan/index.html) to analyze relationships among the main dependent variables (Table S2).

SI Results

Pairwise interactions of land-cover types.

Estimated GCA values of the diallel analysis generally differed among land-cover types (250 m landscapes: $F_{\sim 103,\sim 1600}$=5-46; P<0.001 in all cases; 500 m landscapes: $F_{\sim 68,\sim 192}$=2-18; P<0.001 in all cases; Fig.S2). Furthermore, these GCA values predicted the observed productivity, phenology, albedo and temporal stability quite well and SCA values (i.e. the specific combination of two identical or different land-cover types) explained relatively little amount of additional variance in all cases (with ~163(79) degrees of freedom in the nominator and ~1600(192) in the denominator in the 250m (500m) landscapes dataset, respectively, SCA F-values ranged between 1 and 3; i.e. $F_{\sim 163(79),\sim 1600(192)}$=~1-3; P-values depended on the variables of interest; Fig.S2). Furthermore, we found only two cases where SCA values were significantly influenced by LD in the 500 m landscape dataset, namely $\mathrm{CV}_{\alpha_{\mathrm{vis}}}^{-1}$ and $\mathrm{CV}_{\alpha_{\mathrm{SW}}}^{-1}$, both in which LD lead to a decrease (P<0.05; all other cases: P>=0.05). The SCA's of the different LCC's varied strongly depending on the specific BGR/ALT combination. There was no clear pattern of specific land-cover combinations performing always better or worse than expected (i.e. generally increased or decreased SCA values, respectively). Average SCA values did also not depend on the dissimilarity in average productivity, phenology or temporal stability of the two identical or different constituent land-cover types (P>=0.05 in all cases; Fig. S2).

Landscape structural diversity

Most measures of landscape structural diversity (i.e. edge density (ED), effective mesh size (MESH), Simpson's diversity Index (SIDI), Simpson's evenness index (SIEI) and

patch cohesion index (COHESION); Table S3; McGarigal 2015) were highly correlated with LD (Fig.S3). Of these variables, only ED additionally explained significant amounts of variation in many of the dependent variables when fitted after the LD term in the model (Fig.S3A). In contrast, if ED, MESH and SIDI were fitted as linear contrasts before the LD term, the significance of LD disappeared for many of the dependent variables (Fig.S3B). SIEI showed a smaller correlation with LD, and LD effects were less affected when fitted after SIEI or COHESION compared to the other structural diversity co-variates (Fig.S3B).

Interrelation of primary productivity, phenology and temporal stability

Correlation of primary productivity, phenology and albedo proxies among each other and their link to LD was only tested in the 500 m landscapes dataset, because the 250 m landscapes only cover $\frac{1}{4}$ of the area that influences the corresponding albedo values.

EVI_{GS} was highly correlated with both $\overline{\mathrm{EVI}}$ (Fig.S5A; Pearson's product moment correlation r=0.94, P<0.001) and GSL (r=0.86, P<0.001), whereas α_{SW} was highly determined by α_{NIR} (Fig.S5B; r=0.87, P<0.001) and α_{vis} (r=0.59, P<0.001). Furthermore, the conceptual link between $\overline{\mathrm{EVI}}$ and α_{NIR} also was expressed in the high correlation of these variables (Fig.S5C; r=0.77, P<0.001). Consequently, also $\mathrm{CV}_{\overline{EVI}}^{-1}$ and $\mathrm{CV}_{\alpha_{NIR}}^{-1}$ showed strong correlation (Fig.S5D; r=0.76, P<0.001; all results derived from the 500 m landscapes dataset, n=213). Redundancy analysis (RDA; https://cran.r-project.org/web/packages/vegan/ index.html) showed that LD is most closely related to EVI_{GS},$\overline{\mathrm{EVI}}$, GSL, $\mathrm{CV}_{\overline{EVI}}^{-1}$, $\mathrm{CV}_{\alpha_{NIR}}^{-1}$, $\mathrm{CV}_{\alpha_{vis}}^{-1}$ and $\mathrm{CV}_{\alpha_{SW}}^{-1}$ (Fig. S4). Interestingly, $\mathrm{CV}_{\mathrm{EVI}_{GS}}^{-1}$ clusters closely with CV_{GSL}^{-1} and not with $\mathrm{CV}_{\overline{EVI}}^{-1}$. Furthermore, even though $\overline{\mathrm{EVI}}$ and α_{NIR} are closely correlated (Fig.S5C), they reflect different, well separable qualities of the land surface and are differently influenced by LD (no close clustering of $\overline{\mathrm{EVI}}$ and α_{NIR} in Fig.S4).

Table S1. Effects of landscape diversity (LD) on productivity and phenology proxies, summer land surface albedo, and the over yielding (OY) and temporal stability (CV^{-1}) of these variables. Dependent model terms: landscape functioning variable derived from satellite-remote sensing (Table S2); fixed: the specific fixed terms in the mixed model: BGR: Biogeographic region; ALT: Altitude range; LD: Landscape diversity; fracL: fraction of unproductive land-cover (LC) types in a LC composition; random: the random term was specified by the land-cover type composition (LCC); effect size: coefficient estimates (mean ± s.e.); significance: F-values with associated degrees of freedom and P-values: *: P<0.05; ** P<0.01; *** P<0.001; n.s. not significant; NA: no value. Number of data points in the 250 m landscapes dataset (n) =504; and the 500 m landscapes dataset n=213.

Category	Model terms			Effect of LD					
				250 m extent landscapes (unique LCC n=504)			500 m extent landscapes (unique LCC n=213)		
	dependent	fixed	random	effect size	significance		effect size	significance	
Productivity	EVI_{GS}	BGR+ALT+BGR:ALT+LD+fracL	LCC	0.050 ± 0.019	$F_{1,112}$	= 10**	0.076 ± 0.033	$F_{1,48}$	=7*
	$\overline{EVI}$			0.013 ± 0.004	$F_{1,113}$	= 13***	0.015 ± 0.007	$F_{1,46}$	= 6*
	EVI_{max}			0.016 ± 0.005	$F_{1,114}$	= 13***	0.016 ± 0.009	$F_{1,47}$	= 5*
Phenology	GSL			1.070 ± 0.900	$F_{1,112}$	= 2 n.s.	3.970 ± 1.850	$F_{1,49}$	= 6*
	SOS			0.288 ± 0.500	$F_{1,106}$	= 0 n.s.	-2.405 ± 1.084	$F_{1,44}$	= 6*
	EOS			1.204 ± 0.578	$F_{1,115}$	= 4*	1.611 ± 1.191	$F_{1,54}$	= 2 n.s.
Albedo	α_{NIR}			NA	NA	NA	0.008 ± 0.007	$F_{1,48}$	= 2 n.s.
	α_{vis}						-0.002 ± 0.002	$F_{1,46}$	= 3 n.s.
	α_{SW}						0.001 ± 0.003	$F_{1,47}$	= 0 n.s.
Temporal stability	$CV^{-1}_{EVI_{GS}}$			0.135 ± 0.124	$F_{1,102}$	= 2 n.s.	0.582 ± 0.217	$F_{1,47}$	= 8**
	CV^{-1}_{EVI}			0.477 ± 0.215	$F_{1,104}$	= 6*	1.306 ± 0.474	$F_{1,48}$	=9**
	$CV^{-1}_{EVI_{max}}$			0.380 ± 0.200	$F_{1,107}$	= 5*	0.840 ± 0.343	$F_{1,46}$	= 7*
	CV^{-1}_{GSL}			0.174 ± 0.103	$F_{1,103}$	= 4.	0.610 ± 0.205	$F_{1,48}$	= 10**
	$CV^{-1}_{\alpha_{NIR}}$			NA	NA	NA	1.337 ± 0.661	$F_{1,53}$	= 5*
	$CV^{-1}_{\alpha_{vis}}$						0.031 ± 0.301	$F_{1,55}$	= 0 n.s.
	$CV^{-1}_{\alpha_{SW}}$						1.019 ± 1.051	$F_{1,53}$	= 2 n.s.
Over yielding	$OYEVI_{GS}$		NA	0.053 ± 0.016	$F_{1,370}$	= 11**	0.105 ± 0.046	$F_{1,116}$	= 5*
	$OY\overline{EVI}$			0.012 ± 0.004	$F_{1,370}$	= 8**	0.021 ± 0.011	$F_{1,116}$	= 4*
	$OYEVI_{max}$			0.015 ± 0.005	$F_{1,370}$	= 9**	0.022 ± 0.011	$F_{1,116}$	= 4.
	OY_{GSL}			1.649 ± 0.740	$F_{1,370}$	= 5*	5.443 ± 2.491	$F_{1,116}$	= 5*
	$OY\alpha_{\mathrm{NIR}}$			NA	NA	NA	0.017 ± 0.007	$F_{1,116}$	= 6*
	$OY\alpha_{\mathrm{vis}}$						-0.001± 0.001	$F_{1,109}$	= 1 n.s.
	$OY\alpha_{\mathrm{SW}}$						0.005 ± 0.003	$F_{1,116}$	= 3.

Table S2. The main dependent variables for which we tested LD effects. The columns of the table describe the variable category, the variable name, a short description and the product source, as well as the product source's spatial resolution.

Category	Variable name	Description	Product source, spatial resolution
Productivity	EVI_{GS}	EVI integrated in the growing season (Fig. 1B) averaged for the time 2000-2016	MOD13Q1, 250m and MOD13A1, 500m; Vegetation Indices (Didan 2015)
	$\overline{EVI}$	Average growing season EVI (Fig.1B) averaged for the time 2000-2016	
	EVI_{max}	Maximum growing season EVI (Fig.1B) averaged for the time 2000-2016	
	$OYEVI_{GS}$	Overyielding of EVI_{GS}, i.e. the absolute difference between observed values and expected values of mixture (LD>1) land-cover compositions (LCC) based on averaged values of monoculture (LD=1) LCC's that are constituted of the corresponding land-cover types in the mixture LCC's; see Methods)	
	$OY\overline{EVI}$	Overyielding of $\overline{EVI}$	
	$OYEVI_{max}$	Overyielding of EVI_{max}	
Phenology	GSL	Annual growing season length (days; Fig.1B) averaged for the time 2000-2016	
	SOS	Start of annual growing season (day of year; Fig. 1B) averaged for the time 2000-2016	
	EOS	End of annual growing season (day of year; Fig.1B) averaged for the time 2000-2016	
	OY_{GSL}	Overyielding of GSL	
Albedo	α_{NIR}	Mean annual summer (June-August) albedo integrated over the near-infrared spectrum (wavelengths 0.7–5.0 µm) averaged for the time 2000-2016	MCD43A3, 500m; Albedo product (Schaaf & Wan 2015)
	α_{vis}	Mean annual summer (June-August) albedo integrated over the visible spectrum (wavelengths 0.3–0.7 µm) averaged for the time 2000-2016	
	α_{SW}	Mean annual summer (June-August) albedo integrated over the shortwave spectrum (wavelengths 0.3–5.0 µm) averaged for the time 2000-2016	
	$OY\alpha_{NIR}$	Overyielding of α_{NIR}	
	$OY\alpha_{vis}$	Overyielding of α_{vis}	
	$OY\alpha_{SW}$	Overyielding of α_{SW}	
Temporal stability	$CV^{-1}_{EVI_{GS}}$	Temporal stability of yearly EVI_{GS} in the period of 2000-2016	MOD13Q1, 250m and MOD13A1, 500m; Vegetation Indices (Didan 2015)
	$CV^{-1}_{\overline{EVI}}$	Temporal stability of yearly $\overline{EVI}$ in the period of 2000-2016	
	$CV^{-1}_{EVI_{max}}$	Temporal stability of yearly EVI_{max} in the period of 2000-2016	
	CV^{-1}_{GSL}	Temporal stability of yearly GSL in the period of 2000-2016	
	$CV^{-1}_{\alpha_{NIR}}$	Temporal stability of yearly α_{NIR} (wavelengths 0.7–5.0 µm) in the period of 2000-2016	MCD43A3, 500m; Albedo product (Schaaf & Wan 2015)
	$CV^{-1}_{\alpha_{vis}}$	Temporal stability of yearly α_{vis} in the period of 2000-2016	
	$CV^{-1}_{\alpha_{SW}}$	Temporal stability of yearly α_{SW} in the period of 2000-2016	

Table S3. Landscape structural diversity variables. The columns describe the co-variate name, the spatial resolution and data source, as well as a short description of the co-variate. All definitions were taken from (McGarigal 2015).

Co-variate	Spatial resolution and data source	Co-variate description
Edge density (ED; m^{-1})	100 m spatial resolution of the land-cover product NOAS04 (https://www.bfs.admin.ch)	Total length of edges (borders between two different land-cover types) divided by the total landscape area
Effective mesh size (MESH; m^2)		Sum of the effective mesh size for every land-cover type divided by the total landscape area
Simpson's diversity index (SIDI; no unit)		Simpson's diversity index applied to the number of different land-cover types and their proportional area in the landscape
Simpson's evenness index (SIEI; no unit)		Simpson's evenness index applied to the number of different land-cover types and their proportional area in the landscape
Patch cohesion index (COHESION; no unit)		Average cohesion (i.e. physical connectedness) of land-cover type patches in a landscape

Fig. S1

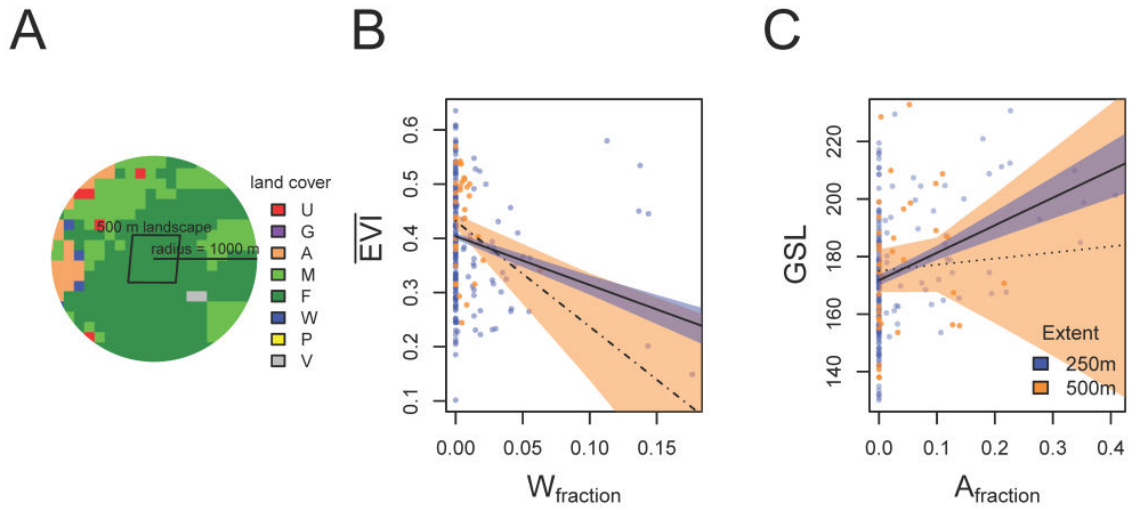

Fig. S1. **Example of a study landscape composed of forest only with its surrounding area (A); change in average growing season EVI ($\overline{EVI}$) of forested landscapes with the fractional cover of water ($W_{fraction}$) in the surrounding area (B) change of growing season length (GSL) of forested landscapes with the fractional cover of agricultural area ($A_{fraction}$) in the surrounding area (C). A.** The example shows a 500 m extent study landscape with its surrounding area with a radius of 1000 m. **B and C.** We tested effects of fractional covers of water ($W_{fraction}$) and agricultural ($A_{fraction}$) area on dependent variables measured for forest land-cover compositions (LCCs; n=187 for 250 m landscapes; n=37 for 500 m landscapes) using the same model structure as specified in the Methods section, but replacing the LD term with the $W_{fraction}$ or the $A_{fraction}$ term, respectively, and removing the fixed term of fracL and the random LCC term. We found that $\overline{EVI}$ of forested landscapes decreased with the fractional cover of water in the surrounding area of 500 m radius for 250 m landscapes ($W_{fraction}$ effect: -0.901 ± 0.189, $F_{1,\ 163}$=23: P<0.001) and marginally so in the surrounding area of 1000 m radius for 500 m landscapes (-1.95 ± 1.06, $F_{1,18}$=3: P<0.1). GSL increased with the fractional cover of agricultural area in the surrounding landscape in 250 m landscapes ($A_{fraction}$ effect: 95.4 ± 25.8, $F_{1,\ 163}$=14: P<0.001) and we found a similar but insignificant trend in 500 m landscapes (21.2 ± 137, $F_{1,18}$=0: P=n.s.).

Fig. S2

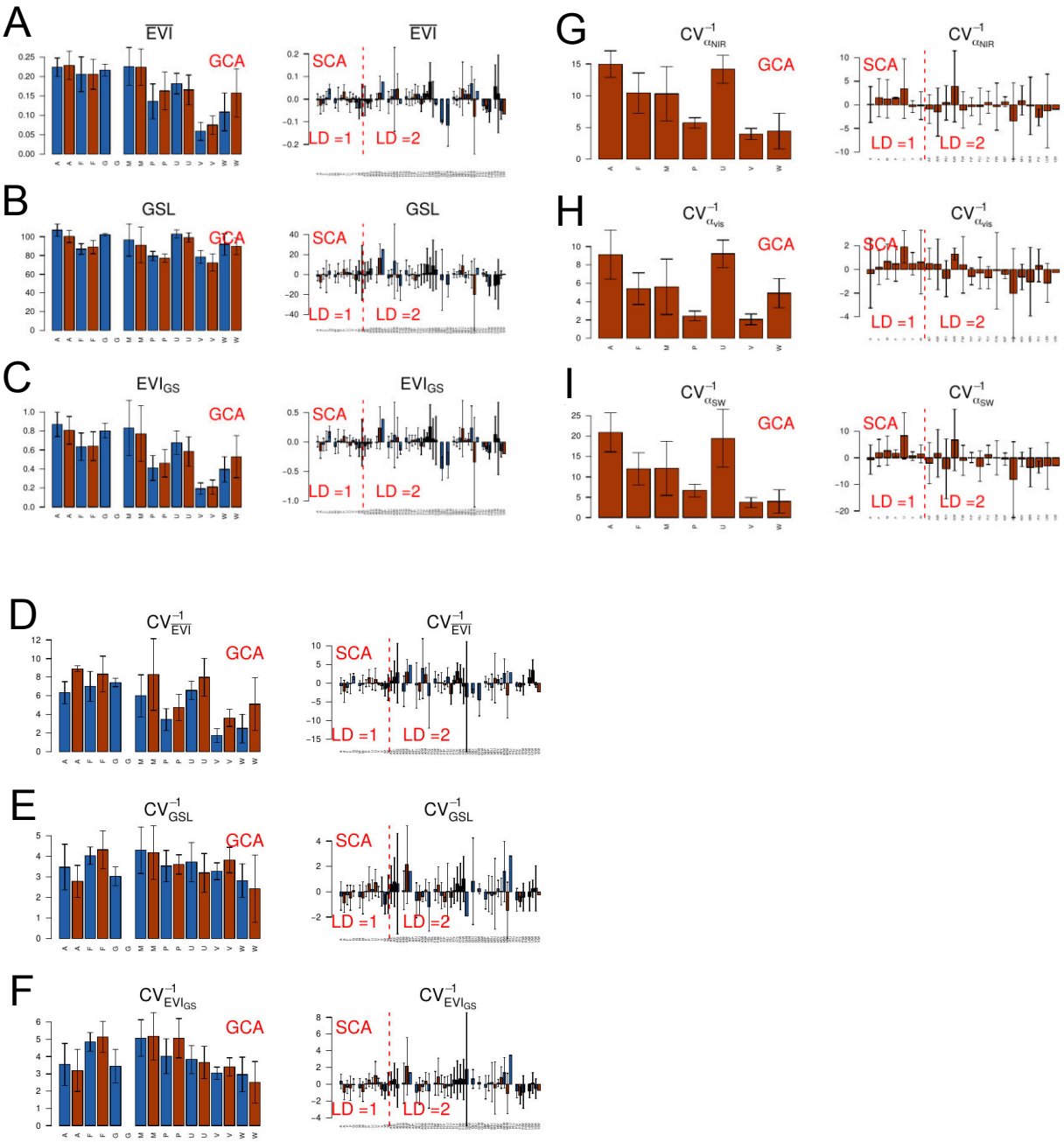

Fig. S2. **Estimated general combining abilities (GCA) and specific combining abilities (SCA) derived from diallel analysis for primary productivity proxies, growing season length (A-C), and temporal stability of productivity, phenology and albedo (D-I).** Bars represent GCA (left panels) and SCA (right panels) values averaged over all blocks of BGR and ALT combinations, for landscapes with 250 m extent (blue, n=504) and 500 m extent (orange, n=213), error bars represent standard errors of the mean. GCA values estimated from the two independent datasets of 250 m and 500 m landscapes generally were in good agreement for the different land-cover types (U: urban; G: urban green; A: arable; M: grass; F: forest; W: water; P: unproductive; V: bare land; 250 m landscapes: $F_{\sim 103,\sim 1600}$=5-46; 500 m landscapes: $F_{\sim 68,\sim 192}$=2-18; P<0.001 in all cases; for all the tested dependent variables). SCA values were

usually smaller than GCA values, did not explain large amounts of additional variance in all cases and depended strongly on the specific combination of biogeographic region (BGR) and altitude range (ALT). We did not find specific land-cover combinations that showed a consistent positive or negative deviation from expected values based on the GCAs.

Fig. S3

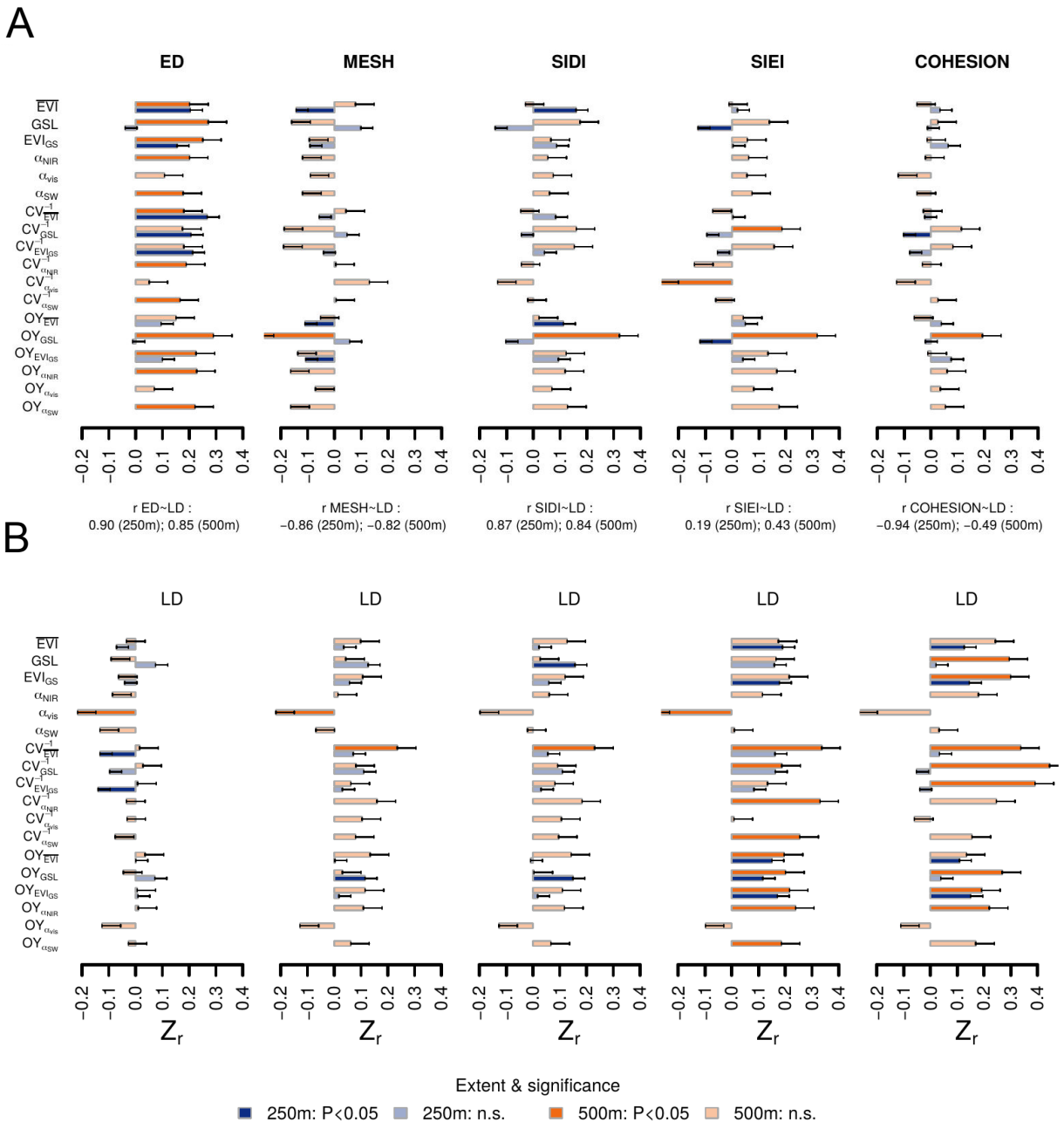

Fig.S3. **Magnitude of effects of landscape structural diversity on the landscape functioning variables after they were fitted as linear contrasts after the LD effect (A) and LD effects when they were fitted as linear contrasts after the corresponding structural diversity measure in A (B).** Bars represent normalized effect sizes (Z_r; see Methods) of LD on different important primary productivity, phenology, albedo and temporal stability variables (see Table S2). The significance (indicated with dark shading [P<0.05] and light shading [P>=0.05]) of the effects is derived from linear mixed-effects models (Methods section) and error bars show standard errors of the mean. All results are derived from the 250 m landscapes dataset (blue; n=504) and the 500 m landscapes dataset (orange; n=213) separately. **A:** LD was highly correlated with ED, MESH, SIDI and COHESION (see Table S3 for independent variable explanations), whereas the correlation was lower for SIEI (r: Pearson's product moment correlation at the

bottom of the graphs in A). Additionally, ED explained high amounts of variation in the dependent variables even when fitted after LD, whereas this was less the case for the other structural diversity measures. **B:** If ED, MESH and SIDI were fitted as linear contrasts before the LD term, LD effect sizes became smaller and effects became insignificant for many of the dependent variables. LD effect sizes and significances stayed, however, relatively unaffected when fitted after SIEI and COHESION.

Fig. S4

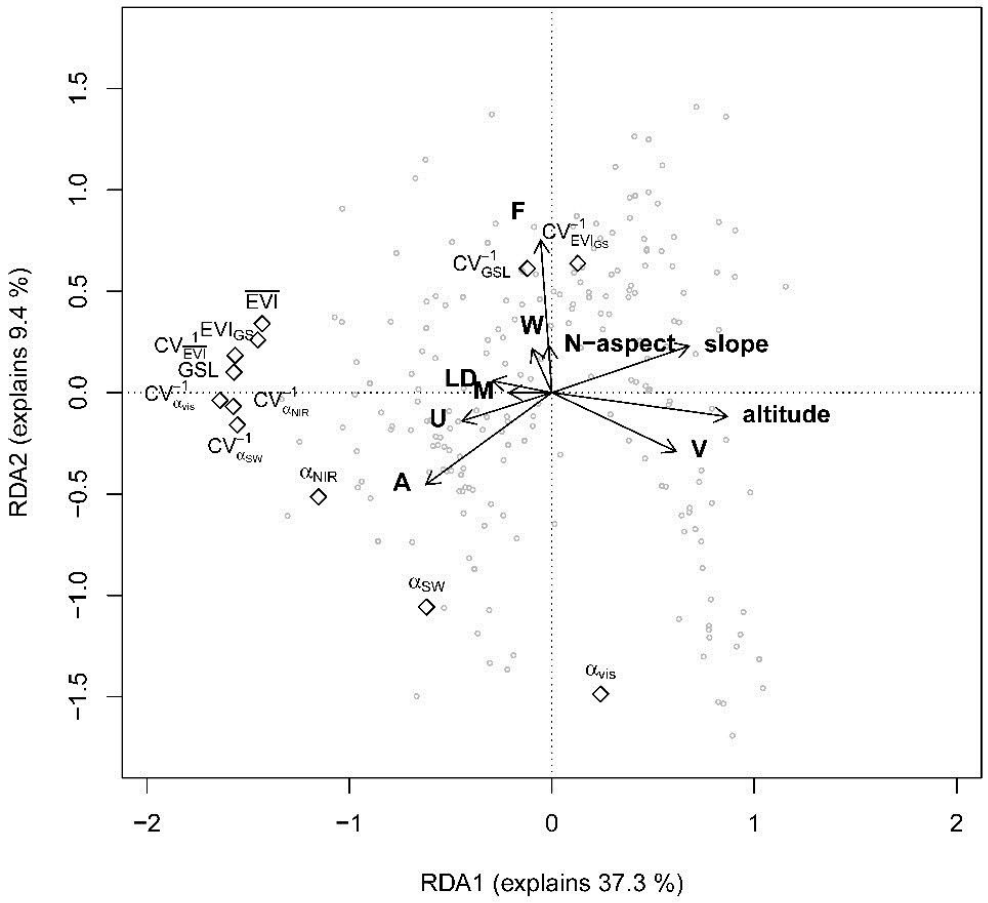

Fig. S4. **Redundancy analysis (RDA; https://cran.r-project.org/web/packages/vegan/index.html) of the main dependent variables of interest (diamond-shaped points), ordinated together with LD and the co-variates used in the landscape plot selection (i,e, altitude, slope, N-aspect and fractional cover of land-cover types (A,F,M,U,V,W; Fig.1).** LD is most closely related to EVI_{GS}, $\overline{EVI}$, $CV_{\overline{EVI}}^{-1}$ and GSL; these variables cluster closely together also with $CV_{\alpha_{NIR}}^{-1}$, $CV_{\alpha_{vis}}^{-1}$ and $CV_{\alpha_{SW}}^{-1}$, but however, EVI and albedo derived measures are still well separable, especially on the RDA2 axis. Interestingly, whereas $CV_{\overline{EVI}}^{-1}$ closely clusters with $\overline{EVI}$, $CV_{EVI_{GS}}^{-1}$ is well separated from EVI_{GS} and strongly clusters with CV_{GSL}^{-1} that exhibits a weak relation with LD. Furthermore, $\overline{EVI}$ and α_{NIR} are well separated on this ordination, which suggests that they represent well separable qualities of the land surface.

Fig. S5

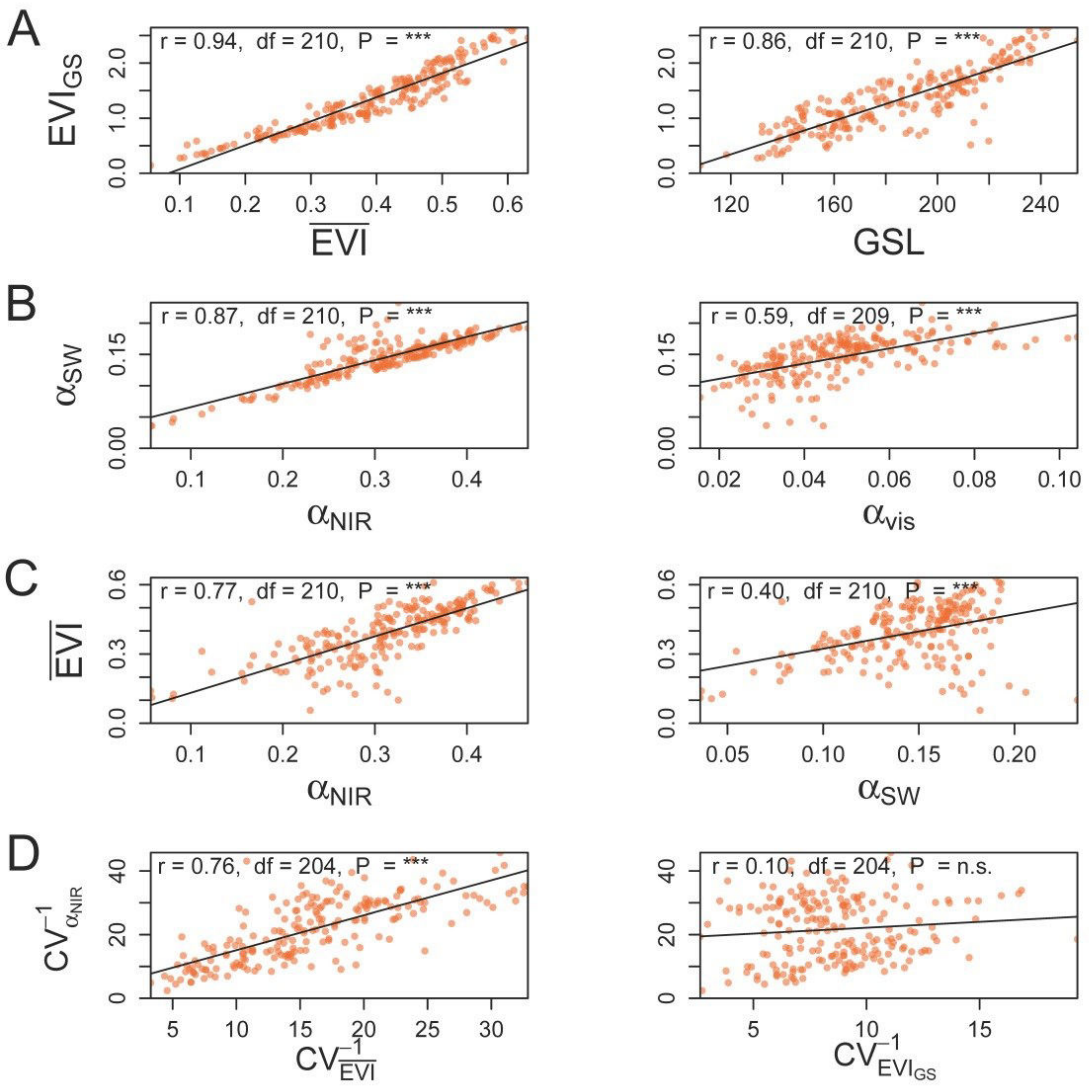

Fig. S5. **Interrelation of primary productivity, phenology, albedo and the temporal stability of these variables. Correlation of EVI_{GS} with $\overline{EVI}$ and GSL (A), α_{SW} with α_{NIR} and α_{vis} (B) $\overline{EVI}$ with and α_{NIR} and α_{SW} (C) and $CV^{-1}_{\alpha_{NIR}}$ with $CV^{-1}_{\overline{EVI}}$ and $CV^{-1}_{EVI_{GS}}$ (D).** The slope of the lines represent Pearson's product moment correlations derived from the 500 m landscapes dataset (n=213), which are further printed on the upper part of the plots (r), together with associated degrees of freedom (df) and p-values (P).*: P<0.05; ** P<0.01; *** P<0.001; n.s. not significant.

Fig. S6

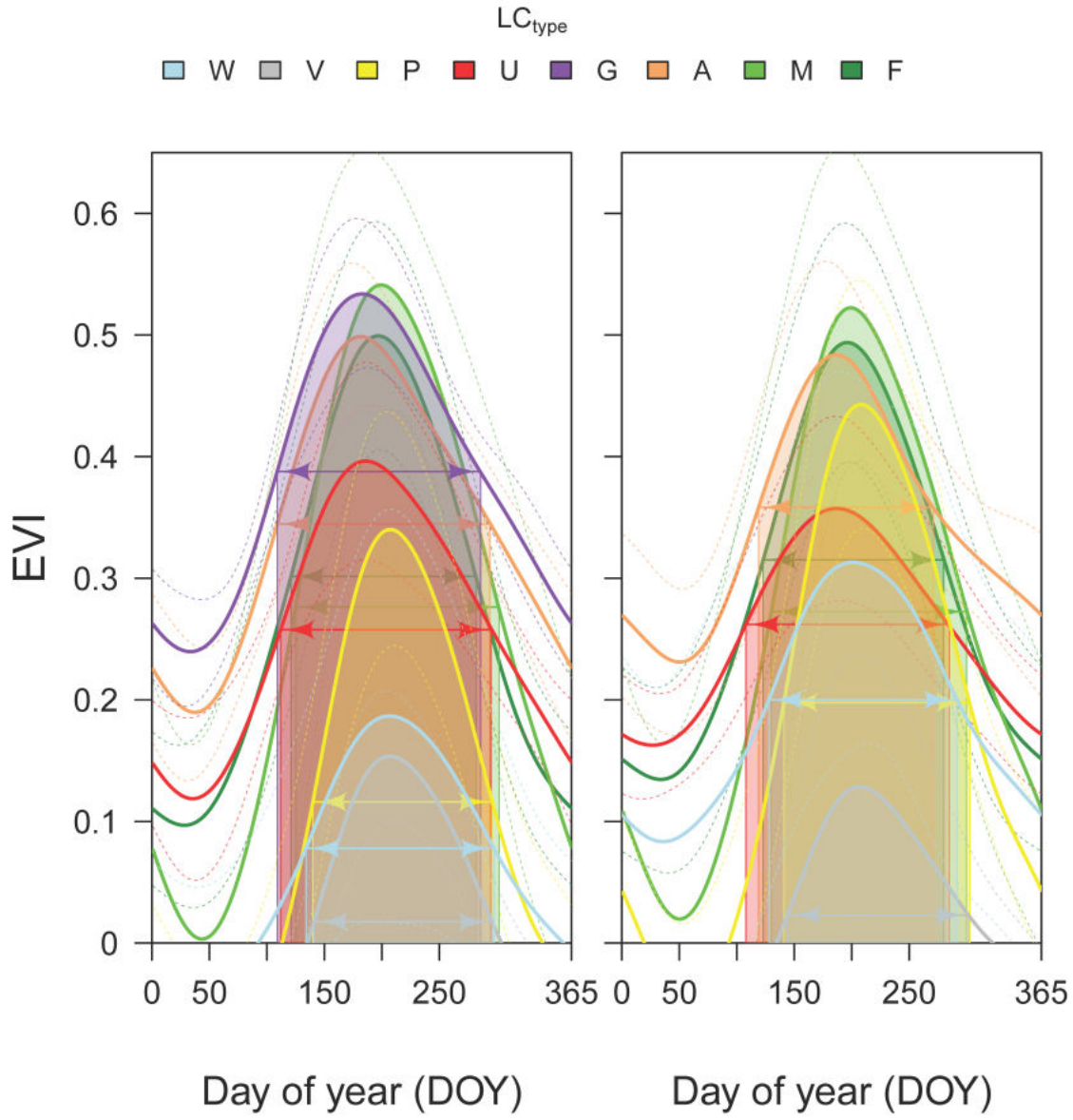

Fig.S6. **Yearly change in vegetation productivity (i.e. EVI) averaged in the time of 2000-2016 for each day of year (DOY; solid lines) and land-cover type (LCtype), in study-landscapes of 250×250 m^2 (left panel, n=106) and study-landscapes of 500×500 m^2 size (right panel, n=69).** Dotted lines represent standard deviations of the averaged values and arrows represent growing season lengths (GSL; Fig.1B). A: arable, F: forest, G: urban green, M: grass, P: unproductive, U: urban, V: bare land, W: water.

Chapter 3: Biodiversity promotes primary productivity and growing season lengthening at the landscape scale

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A diverse landscape, photographed in Schwarzenberg, LU.

Biodiversity promotes primary productivity and growing season lengthening at the landscape scale

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Experiments have shown positive biodiversity-ecosystem functioning (BEF) relationships in small plots with model communities established from species pools typically comprising few dozen species. Whether patterns found can be extrapolated to complex, nonexperimental, real-world landscapes that provide ecosystem services to humans remains unclear. Here, we combine species inventories from a large-scale network of 447 1-km^2 plots with remotely sensed indices of primary productivity (years 2000–2015). We show that landscape-scale productivity and its temporal stability increase with the diversity of plants and other taxa. Effects of biodiversity indicators on productivity were comparable in size to effects of other important drivers related to climate, topography, and land cover. These effects occurred in plots that integrated different ecosystem types (i.e., metaecosystems) and were consistent over vast environmental and altitudinal gradients. The BEF relations we report are as strong or even exceed the ones found in small-scale experiments, despite different community assembly processes and a species pool comprising nearly 2,000 vascular plant species. Growing season length increased progressively over the observation period, and this shift was accelerated in more diverse plots, suggesting that a large species pool is important for adaption to climate change. Our study further implies that abiotic global-change drivers may mediate ecosystem functioning through biodiversity changes.

ecosystem function and services | EVI and NDVI land surface phenology | large spatial scale | nonexperimental, real-world ecosystems | plant, bird, and butterfly species richness

Field and laboratory studies in which the diversity of plant species was experimentally manipulated have demonstrated that species loss can decrease many ecosystem functions including primary productivity (1) and its temporal stability (2). These biodiversity-ecosystem functioning (BEF) studies have revealed generally positive effects of species richness on primary productivity and also shed light on the mechanisms that promote productivity under these conditions (3). Niche differentiation among species can enhance community-level productivity through complementary resource use, decreased competition (3), and reduced density-dependent herbivore and pathogen pressure (4). Facilitation can increase community-level productivity via positive effects of one species on another. For example, legumes often symbiotically fix atmospheric dinitrogen which subsequently becomes available also to nonlegume species (3). Finally, positive sampling effects occur if more diverse communities include species with high productivity and these species reach dominance (3). Although there is considerable variability among the ecosystems investigated, biodiversity effects on primary productivity generally are substantial with metaanalyses showing that they can be as large as effects of other drivers of environmental change such as drought, fire, or eutrophication (5, 6).

Field experiments in which the diversity of communities is manipulated can only address effects that occur at the scale of small plots (typically <100 m^2), and in newly created ecosystems over relatively short periods of time (7). Also, the communities used in these studies typically are comprised of a random selection of species from relatively small species pools of one trophic group of organisms, in most cases plants (7). These settings markedly contrast conditions in nonexperimental, natural, or seminatural, "real-world" ecosystems (8). In such systems, the diversity of multiple trophic groups often varies in concert (9) and the composition of communities is determined by nonrandom community assembly processes (8). Nonexperimental ecosystems typically are more complex and closer to steady state than experimental plots in which plant species assemblages often need to be maintained by regular weeding (10). Finally, experimental studies, even if they are repeated across large geographic scales (11), lack the landscape-scale environmental context (e.g., heterogeneity, environmental adversity, species pool) that may influence BEF relationships (12).

The dramatic loss of diversity both globally (13) and in many places also locally (14) is one of the most pressing environmental problems of our time (15). Real-world ecosystems provide critical ecosystem services to humans (16), and it therefore is crucial to evaluate whether the consequences of species loss identified in BEF experiments also hold under complex natural and seminatural conditions. Here, we used 447 plots 1 km^2 in size and spread regularly across six biogeographic regions (BGR) and an altitude range of 249–2,819 m above sea level (a.s.l.) in Switzerland (Central Europe) to evaluate whether plant productivity is related to the biodiversity found in these plots (Fig. 1 and *Materials and Methods*). The species diversity of vascular plants, breeding birds, and butterflies was obtained from surveys carried out twice in 2001–2013 in the frame of a national biodiversity monitoring program (BDM; ref. 17; biodiversitymonitoring.ch). Proxies of primary productivity were derived from satellite-sensed

Significance

Research of the past decades has shown that biodiversity promotes ecosystem functions including primary productivity. However, most studies focused on experimental communities at small spatial scales, and little is known about how these findings scale to nonexperimental, real-world ecosystems at large spatial scales, despite these systems providing essential ecosystem services to humans. Here, we show that primary productivity, its temporal stability, and the decadal trend of a prolonged growing season strongly increase with biodiversity across heterogeneous landscapes, which is consistent over vast environmental, climatic, and altitudinal gradients. Our findings thus underline the critical role biodiversity plays for ecosystem functioning and responses to environmental change in heterogeneous, real-world ecosystems at the landscape scale.

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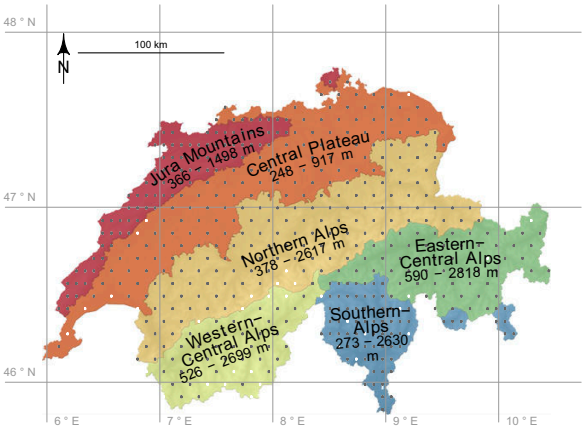

Fig. 1. Swiss BDM sampling design. Dots represent a systematic grid of 509 plots, each 1 km^2 in size, spanning six BGRs (names and altitude ranges shown in map). A denser sampling grid is used in the Jura Mountains and Southern Alps because of their smaller area. For our analysis, we used a subset of 447 plots (gray).

vegetation indices [Moderate Resolution Imaging Spectroradiometer enhanced vegetation index (MODIS EVI); ref. 18]. Specifically, we tested whether landscape-scale biodiversity measures of plant, bird, and butterfly communities promoted our proxy of primary productivity, and its temporal stability. Capitalizing on the high spatial and temporal resolution of the productivity data, we analyzed whether these effects were caused by higher momentary vegetation activity, or by an extended growing season. We further tested whether growing season length (GSL) increased throughout our observation period, and whether this change depended on biodiversity. Finally, we evaluated the magnitude of all biodiversity effects in relation to the magnitude of effects of other drivers related to climate, topography, and land cover.

Results

Primary Productivity. We derived two proxies of primary productivity from a remotely sensed vegetation activity index (MODIS EVI; see *Materials and Methods* for details). $\overline{EVI}$ characterizes average growing season productivity, whereas EVI_{GS} integrates EVI over the growing season, i.e., also factors in changes in GSL (Fig. 2). We ran all analyses for both $\overline{EVI}$ and EVI_{GS} but only report results for EVI_{GS} because effects were very similar for both dependent variables. EVI_{GS} increased strongly with the diversity of vascular plants (S_{plants}; Fig. 3*B*; $F_{1,378} = 172$, $P < 0.001$). A similar effect was found when using an index (S) that combined the diversity of all taxa using an ordination technique (Fig. 3*A*; $F_{1,379} = 240$, $P < 0.001$). The study area was composed of distinct BGRs (Fig. 1). Biodiversity differed among BGR and was negatively correlated with altitude (Pearson's product moment correlation $r = -0.48$ for S and $r = -0.50$ for S_{plants}), leading to a partial confounding of effects. Estimated effects of biodiversity became smaller when adjusted for altitude (Fig. 3 *A* and *B*; solid lines) or BGR but remained highly significant for both S and S_{plants} (Table S1). Biodiversity effects were independent of altitude and BGR [interaction of S and S_{plants} with BGR and with altitude: not significant (n.s.)]. We also included covariates related to topography, climate, and land cover into our models (Table S2), but similar to BGR and altitude, effects of biodiversity remained highly significant even when fitted after these terms (effect sizes: Table S1).

Temporal Stability of Primary Productivity. We quantified the temporal stability of productivity as the inverse coefficient of variation of EVI_{GS} in the years 2000–2015 ($CV^{-1}_{EVI_{GS}}$). This metric increased strongly with biodiversity (S: $F_{1,445} = 45$, $P < 0.001$; S_{plants}: $F_{1,444} = 43$, $P < 0.001$; Fig. 3 *C* and *D* and Table S1). Biodiversity remained statistically significant when fitted after altitude (S: $F_{1,438} = 35$, $P < 0.001$; S_{plants}: $F_{1,443} = 33$, $P < 0.001$; Fig. 3 *C* and *D* and Table S1), but altitude explained no additional variation when fitted after biodiversity. Effects of biodiversity also were independent of altitude (S × altitude and S_{plants} × altitude: n.s.).

Long-Term Changes in Growing Season Length. The 16-y average GSL (*Materials and Methods* and Fig. 2) decreased with altitude, but showed no effect of biodiversity after accounting for altitude. However, GSL increased by 0.39 ± 0.07 d·y^{-1} over the observation period ($F_{1,996} = 34$; $P < 0.001$), and this rate of change was significantly accelerated with biodiversity (Fig. 3 *E* and *F*; S: $F_{1,444} = 18$, $P < 0.001$; $S_{plants:}$ $F_{1,442} = 19$; $P < 0.001$; Table S1). This diversity effect on growing season prolongation was mediated by effects on start of season (SOS; Fig. 2; S: $F_{1,428} = 60$, $P < 0.001$; S_{plants}: $F_{1,424} = 58$; $P < 0.001$), with no parallel effect on end of season (EOS; Fig. 2; S and S_{plants}: n.s.). The biodiversity effects on the rate of change of SOS and GSL were independent of altitude (S × altitude and S_{plants} × altitude: n.s.), and, notably, the rates of change of SOS and GSL were similar across all altitude ranges.

Magnitude of Biodiversity Effects. While climatic, topographic, and land cover-related covariates explained some variance in our data, the metaanalytic effect sizes (Z_r values derived from F statistics in linear models; ref. 19) of both overall and altitude-corrected biodiversity effects were among the largest of all tested explanatory variables (Fig. 4), for all biodiversity metrics.

Effects of climatic covariates on EVI_{GS} (Fig. 4*A*) were largely altitude-mediated, i.e., their effects vanished when adjusted for altitude. This was to some extent also the case for topographic and land cover-related covariates. Our biodiversity variables were much less confounded with altitude. Very similar patterns were found for the stability of productivity (Fig. 4*B*) and growing

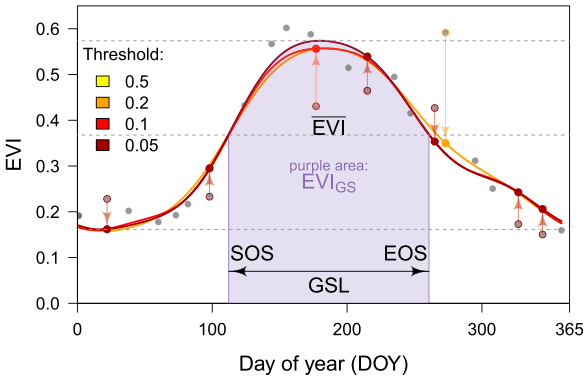

Fig. 2. Example of a 1-y EVI time series and the metrics derived from this data. Original EVI data (gray dots) were approximated as sum of three harmonics (dark-red line). In a step-wise process, data exceeding given thresholds were replaced with model predictions (arrows). See *Materials and Methods* for details. From the final fit, we derived GSL, start and end of growing season (SOS and EOS), and the proxies of primary productivity growing-season EVI ($\overline{EVI}$) and the integral of EVI over the growing season (EVI_{GS}). Over all years and plots, $\overline{EVI}$ averaged 0.42 and EVI_{GS} averaged 0.23, corresponding to a gross (net) primary productivity of 970 (896) g of C·m^{-2}·y^{-1} for the same time and area (MODIS MOD17A2H and MOD17A3H products; ref. 54).

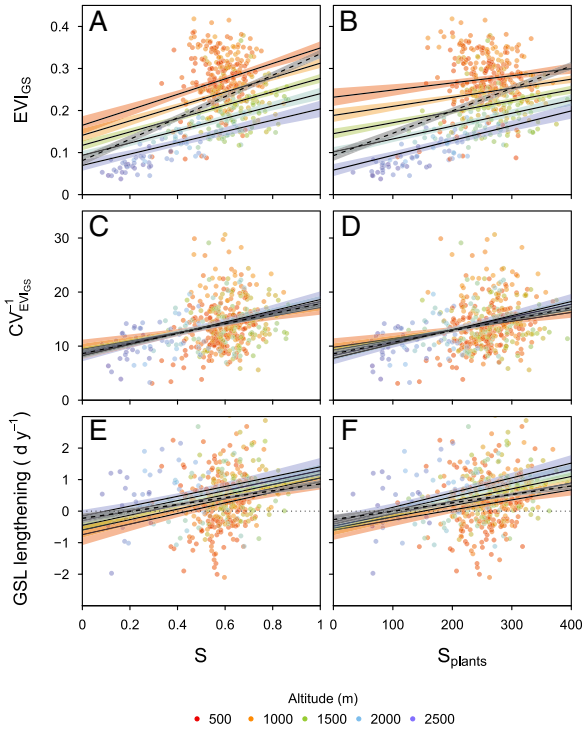

Fig. 3. Biodiversity effects on primary productivity (proxy: EVI_{GS}; *A* and *B*), its temporal stability ($\mathbf{CV}^{-1}_{\mathbf{EVI_{GS}}}$; *C* and *D*), and on the trend in growing season lengthening in 2000–2015 (GSL-lengthening; *E* and *F*). Effects were tested using an indicator combining the species richness of several taxa (S: plants, birds, butterflies), or of vascular plants alone (S_{plants}). Dashed lines, overall effects; solid lines, model predictions for given altitudes; shaded areas, SEs of model predictions; $P < 0.001$ for all effects of biodiversity; $n = 447$ plots; see Table S1 for models and *F* statistics.

season lengthening (Fig. 4*C*) except that altitude had much less of an effect, i.e., overall and altitude-corrected effects were similar in size for most of the explanatory variables.

Interrelation of Drivers. Structural equation models (SEM) showed that biodiversity (S) was positively related to primary productivity (EVI_{GS}) and GSL [Fig. 5*A*; $P(\chi^2_3) = 0.5$]. Effects of S on EVI_{GS} followed two paths: First, EVI_{GS} increased because of positive effects mediated by a higher growing season vegetation activity ($\overline{EVI}$; standardized path coefficient of 0.14, $P < 0.001$); second, EVI_{GS} also increased because of indirect, positive effects through an increase in GSL (standardized path coefficient of 0.21, $P < 0.001$). This SEM explained 82% and 62% of the variation in EVI_{GS} and GSL, respectively. Additional SEM (Fig. S1) without indirect path from S through GSL showed significant positive links from biodiversity (S) to EVI_{GS}, the stability of productivity ($CV^{-1}_{EVI_{GS}}$), and GSL lengthening, and support the notion that primary productivity was in part promoted by S through enhanced temporal stability but not through growing season lengthening. The exogenous variables in our SEM were correlated, some highly (Fig. 5*B*). However, path coefficients for biodiversity were in the same range as coefficients of other exogenous variables, indicating that substantial amounts of the overall effects were simultaneously driven by multiple drivers, of which S was a very important one.

Biodiversity and land-cover richness ($LC_{richness}$), a measure of landscape diversity, were positively correlated (Pearson's product moment correlation; S: $r = 0.36$; S_{plants}: $r = 0.35$). We fitted SEMs with the additional exogenous variable $LC_{richness}$. However, including $LC_{richness}$ did not decrease path coefficients for S. We also tested whether effects of diversity depended on $LC_{richness}$ but this was not the case ($S \times LC_{richness}$: n.s. in linear mixed models).

Discussion

Our analysis indicates that biodiversity is tightly linked to primary productivity and its temporal stability in large field plots spanning extensive environmental, climatic, and topographic gradients in Switzerland (Central Europe). Our plot network contrasts markedly with biodiversity experiments with respect to size, structural complexity, and age of the communities investigated. The effects we report here nevertheless are comparable to the ones observed in experimental studies in small plots, suggesting that the positive effects of biodiversity on ecosystem functioning, in particular on productivity, also exist in real-world landscape-scale ecosystems that integrate different land cover types (i.e., metaecosystems; ref. 20).

Drivers of primary productivity generally are correlated in nonexperimental studies of BEF relationships across natural landscapes (21–23). The individual contributions of these drivers thus are difficult to disentangle. The amount of explained variance shared by potential explanatory variables can be explored with methods that include multiple regression models, path analysis, or variance partitioning schemes. However, even if applied in an educated way these methods can only suggest likely boundaries for effect sizes and do not allow an unequivocal attribution of effects to particular drivers or mechanisms. In our study, altitude was the primary factor that explained variation in productivity and was negatively correlated with biodiversity. Comparing the biodiversity effects on productivity that we found to findings from experiments therefore remains difficult. Meta-analytic normalized effect sizes (Z_r) were in the range of ~0.4–0.8 for overall effects of biodiversity and shrank to 0.3–0.4 when first adjusted for altitude. These Z_r values place the biodiversity effects in our study above the median response reported for primary producers in the metaanalysis of ref. 1.

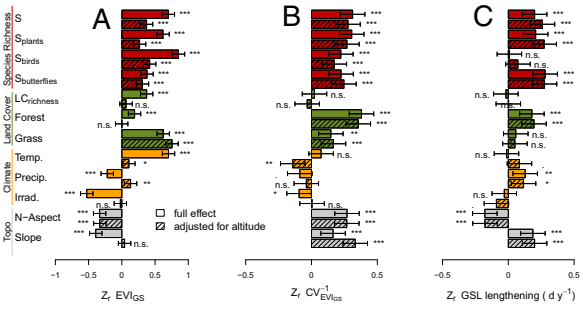

Fig. 4. Magnitude of effects of biodiversity, land cover, and climatic and topographic drivers of productivity (*A*; EVI_{GS}), the temporal stability of productivity (*B*; $\mathbf{CV}^{-1}_{\mathbf{EVI_{GS}}}$), and growing season lengthening over the 2000–2015 observation period (*C*). Data show normalized effect sizes (z-transformed, based on *F* ratios) as used in metaanalysis, with (hashed bars) or without (white bars) prior correction for effects of altitude. Biodiversity ranged among the variables with the largest effect sizes, irrespective of adjustment for altitude. Forest and Grass, fraction of plot covered by forest or grassland; $LC_{richness}$, number of land cover types in plot; for details see *SI Materials and Methods* and Table S2. Error bars show 95% confidence intervals; $n = 447$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; see Table S1 for models and *F* statistics. Irrad., annual shortwave irradiation; N-aspect, North-south component of aspect; Precip., annual precipitation; Slope, average slope; Temp., mean annual temperature.

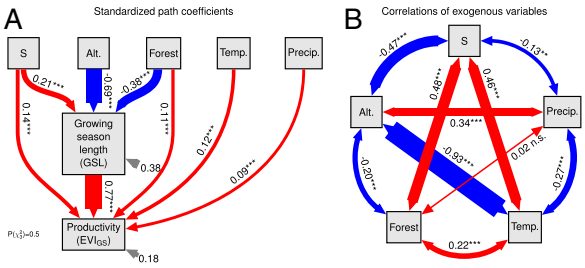

Fig. 5. Path diagram of effects of biodiversity on productivity (EVI_{GS}) that are mediated by or independent of changes in GSL. The structural equation model accounts for altitude (Alt.), and variables related to land cover and climate. Standardized path coefficients (*A*) and correlation of exogenous variables (*B*) are shown separately. Other drivers were tested but removed from the model because they had no statistically significant path coefficients. Gray arrows, residual variances; $n = 447$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. See Fig. S1 for additional structural equation models including $CV^{-1}_{EVI_{GS}}$ and GSL lengthening. Forest, fraction of plot covered by forest; Precip., annual precipitation; Temp., mean annual temperature.

BEF relationships in experiments have been attributed to mechanisms that include so-called complementarity and sampling effects (3). We cannot disentangle these mechanisms in our data because we cannot break down community-level or even metaecosystem-level vegetation indices into contributions from individual species. However, the pattern we found integrates effects over several hundred communities with nearly 2,000 vascular plant species from different habitats. The communities we investigated (on average 250 plant species per study plot) therefore did not share a common species set, and we did not find evidence that responses were driven by a few particular species.

Biodiversity was linked to an increased temporal stability of primary productivity, which again suggests that BEF relationships observed in experiments with small plots (2) also apply in natural systems at the landscape scale. Effects on stability have traditionally been expressed as resistance to or resilience from disturbance. Our study included extreme events such as the extreme heat wave and drought in summer 2003 (24). However, this driver did not affect our study network homogeneously, with more severe impacts at low altitude and positive effects in alpine areas (25). Given that biodiversity was generally higher at low altitude, i.e., in areas that were particularly badly affected by this heat wave, we would have expected such altitude-dependent disturbance effects to mask positive effects of biodiversity rather than to promote them.

It has been argued that biodiversity effects in experiments originate in part from poorly performing low-diversity communities that typically result from random species selection (26) and regular weeding (10). In our study, agricultural land typically was species-poor and often periodically bare or low in ground cover, similar to the situation in experiments. To test whether our findings were biased by the presence of agricultural land, we repeated all analyses excluding plots that contained agricultural land (*SI Materials and Methods*); however, the pattern of positive BEF relationships remained (Figs. S2 and S3), supporting the idea that poorly performing low diversity plots were less important in the real-world landscapes we investigated. The strong biodiversity effects we found thus are all the more remarkable.

The biodiversity effects on productivity and its temporal stability were statistically robust. They remained highly significant when we repeated our analyses accounting for the presence or abundance of any particular land-cover type, indicating that they did not originate from a confounding of biodiversity with any particular land-cover type (Table S1). These effects also were consistent across the different biogeographic regions and altitudes of Switzerland.

Positive biodiversity effects on primary productivity were in part driven by changes in GSL, i.e., overall effects resulted not only from increased but also from prolonged vegetation activity. Our findings show that biodiversity also was related to an enhanced longer-term (decadal) trend toward a prolonged growing season. Global observations of trends in vegetation phenology indicate an earlier onset of vegetation activity in spring and a delayed senescence in fall for many locations (27). These phenological shifts are generally attributed to warming, which is typically more pronounced at higher altitudes (28). The capacity of species to adapt their phenology to climate change is important for their survival, in particular when species are unable to migrate to other habitats with suitable climate (29). Studies have shown that variation in phenology allows for the coexistence of species through temporal complementarity (30). Conversely, our results promote the idea that high biodiversity provides a greater capacity for plant communities to respond to emerging opportunities for activity and growth in the shoulder season. In other words, climate warming seems to create additional environmental niche space that can be filled, given a sufficiently large source species pool (31). Hence, our study provides evidence that biodiversity is a critical determinant of the phenological sensitivity (29) of communities and, thus, also the long-term performance of ecosystems in real-world landscapes. Biodiversity mediated growing season lengthening by shifting the start but not the end of the season. One possible interpretation is that the start of season phenology in vascular plants is more strongly linked to temperature, and to processes regulated by species-specific, variable genetic pathways (e.g., genes related to responses to winter-chilling; ref. 32). In contrast, the regulation of end of season is related to a more complex interplay of multiple environmental cues and conserved ontogenetic factors common to most plant species, which will limit the potential for community-level changes with species composition and diversity (32). Irrespective of the mechanisms involved, the effects we report here are large, with biodiversity substantially modulating decadal trends in season lengthening. We therefore argue that considering biodiversity may help to understand and predict community-level trends in phenology, irrespective of the underlying variable, idiosyncratic, or context-dependent responses of individual species, which are challenging to predict (33).

Evergreen and deciduous vegetation exhibit different seasonal amplitudes in EVI. In our study, the fraction of evergreen forest increases with altitude. To rule out the possibility of related biases on our estimates of GSL, we reanalyzed a subset of the original data, where study plots with 10% or more forested area classified as "deciduous" or "mixed-deciduous" were excluded (*SI Materials and Methods*). However, phenology estimates did not change and BEF patterns stayed similar (Figs. S2 and S3).

An advantage of observational studies is that they involve more realistic conditions than experiments in which community composition is directly manipulated. However, a caveat of the observational approach is that the directionality of effects cannot be inferred with certainty. Early studies relating biodiversity and primary productivity across habitats have coined the concept of a hump-shaped relationship with high biodiversity at intermediate productivity (34). This has been explained by resource limitation in low-productivity environments and competitive exclusion (34), or reduced heterogeneity of limiting resources in high-productivity environments (35). Empirical evidence for this hump-shaped relationship is mixed, in part possibly because it is confounded with other important drivers of productivity and diversity (36). Such drivers include biogeographic constraints on the species pool, spatial heterogeneity, and disturbance (37). We have deliberately analyzed effects of biodiversity on primary productivity, which is the perspective adopted in BEF experiments. Our study nevertheless remains correlational, and a reverse causality or a common third cause are also conceivable. For example, positive effects of resource availability on both diversity and productivity may have occurred in marginal environments such as alpine regions. However,

agricultural activities in regions such as the Swiss central midlands have led to large-scale nitrogen deposition from airborne transport of volatilized fertilizer nitrogen (38). Similar effects are found from rainout of air pollution from traffic and fossil fuel-based heating along the pre-Alps (39). In such areas, species loss may be found as a consequence of eutrophication, which would go along with a negative rather than positive biodiversity–productivity relationship due to competitive exclusion. Given that biodiversity may have simultaneously acted as driver of and response to productivity, the overall net relation we observed here might ultimately underestimate the importance of biodiversity in promoting productivity. Assuming that effects of productivity on biodiversity would dominate and result in a positive correlation of the two would be inconsistent with the hump-back model. The positive effects of biodiversity on the temporal stability of productivity and the lengthening of the growing season provide additional support for at least a strong partial cause–effect directionality from biodiversity to productivity at the landscape scale.

As is typical in observational studies, effects of the different drivers we inspected were not fully independent. Hence, effects of environmental drivers of productivity were partly mediated via biodiversity (and vice versa), in line with earlier studies (40, 41). Despite dominant influences of altitude-related climatic effects, residual effects of biodiversity on productivity and season lengthening were substantial. These large landscape-scale effects of biodiversity extrapolate similar evidence from experimental studies that show that biodiversity can be as important as other drivers of global change (5, 6).

The combined diversity of the different taxa (S) often explained more variation in the analyzed variables than plant species richness alone (S_{plants}). This supports the idea that the diversity of taxa other than plants reflects elements of plant species richness that were not captured in the vegetation surveys, or that these metrics are indicative of independent properties of the investigated ecosystems that are relevant for their functioning (e.g., structural complexity; ref. 42).

In conclusion, we demonstrate that biodiversity effects can be found at large spatial scales in real-world ecosystems. These effects are at least as large as the ones reported from small-scale experimental systems, despite different community assembly processes at play. Ecosystem services are provided in real-world landscapes and are of enormous economic value (16), which has raised concerns about whether they will be maintained at current levels, given the ongoing, unprecedented rates of biodiversity loss (13). Our results indicate that biodiversity indeed is critical for the provision of these ecosystem services. We show that, in real landscapes, biodiversity is as important as other environmental drivers, including climate, land cover, and topography. For example, we provide evidence that climate change translates more effectively into a longer growing season and, therefore, productivity when a sufficiently large species pool is available. Ultimately, this implies that, if global environmental change affects the composition of biological communities, a significant part of the overall effect of these changes may be a biodiversity effect in disguise.

Materials and Methods

Study Design. We used a systematic network of 447 plots of 1×1 km in size that are part of the Swiss Biodiversity Monitoring Program (BDM; ref. 17). These plots are systematically spread across the entire 41,248 km^2 of Switzerland and cover six biogeographic regions that form distinct units with respect to climate, edaphic conditions, and distribution patterns of fauna and flora (ref. 43 and Fig. 1). After excluding plots without vegetation (e.g., lakes, snow fields, scree slopes) or insufficient remote-sensing data, of the original 509 BDM plots, a total of 447 plots with complete data and spanning an altitudinal range of 249–2,819 m a.s.l. remained for our analysis.

Biodiversity. In each 1-km^2 plot, vascular plant and butterfly species were monitored along 2,500 × 5 m transects following standardized field protocols (44). Breeding bird species were monitored along a plot-specific route with an average length of 5 km following the standardized method of the Common Breeding Bird Survey (45). Monitoring events took place in 5-y intervals. We derived average species richness from the first two monitoring events in 2001–2013. This procedure revealed the presence of 1,931 vascular plant, 152 breeding bird, and 188 butterfly species in the 447 1-km^2 study plots.

Since primary productivity is largely driven by plants, we focused on vascular plant species richness (S_{plants}) as a measure of biodiversity. We expected the species richness of breeding birds (S_{birds}) and butterflies ($S_{butterflies}$) to reflect additional aspects of the overall biodiversity and the structural complexity of biotic communities (42) in the plots, which may also be relevant for ecosystem functioning. We therefore calculated an aggregated indicator of the biodiversity of all taxa (S), which we obtained from the first ordination axis of a principal component analysis combining the species richness of all three taxa. This axis explained 63% of the variation in the species richness data, with loadings of 0.69, 0.55, and 0.47 for vascular plant, breeding bird, and butterfly species richness, respectively. To simplify the interpretation of this biodiversity metric, we rescaled the ordination axis so that values of zero and one corresponded to the complete absence of species and to the simultaneous presence of the maximum number of plant ($n = 394$), bird ($n = 57$), and butterfly ($n = 78$) species that were found in any plot.

Primary Productivity and Growing Season. We derived growing season vegetation activity and GSL from satellite-borne data (MODIS; ref. 18) with a spatial resolution of ≈250 m and a temporal resolution of 16 d. We used the EVI, which, similarly to the normalized difference vegetation index (NDVI), quantifies photosynthetically active vegetation from the ratio of red and near-infrared reflected light but uses blue band data to correct for scattering by aerosols (46). EVI time series were smoothed using a modified implementation of the harmonic analysis of time series algorithm (HANTS; ref. 47) (Fig. 2, and *SI Materials and Methods*). Many methods exist to determine growing season start (SOS), end (EOS), and length (GSL) from remote sensing data (48), with no universally accepted best approach (49). We used the $NDVI_{ratio}$ method (50), which defines SOS as day of year at which EVI first exceeded the mean of its annual minimum and maximum value. Similarly, EOS indicates the first day of the year at which EVI fell below this threshold. This method is widely applied (48), yields results that are consistent with ground-measured plant phenology (49), and is robust with regard to different annual shapes of vegetation activity (51). Average growing season vegetation activity ($\overline{EVI}$), a first proxy of primary productivity, was estimated as average EVI in the SOS to EOS time span. A second proxy, EVI_{GS}, integrates EVI values over the growing season:

$$EVI_{GS} = \int_{SOS}^{EOS} EVI(t)dt = \overline{EVI}(EOS - SOS). \quad [1]$$

We quantified the temporal stability of primary productivity as reciprocal coefficient of variation of yearly EVI_{GS} for the years 2000–2015 ($CV^{-1}_{EVI_{GS}}$). We also derived the temporal trend in seasonality (SOS, EOS, and GSL) over the 16-y period by linearly regressing these data against time. EVI-derived data were mapped to the 1-km^2 study plots by computing area-weighted means for potentially vegetated land surfaces (i.e., excluding water, rock, glaciers) in each 1-km^2 plot and year.

Land Cover, Topography, and Climate. For each 1-km^2 plot, covariates related to land cover, topography, and climate were determined (see *SI Materials and Methods* for details). In brief, land-cover information was derived from point data with 100-m spatial resolution. We classified each point into eight classes (forest, grassland, agricultural, urban, urban green, water, unproductive, bare land) and calculated their fractional cover in each 1-km^2 plot. Land-cover richness ($LC_{richness}$) was determined as number of land cover types present. Topographic data (mean plot value of altitude, slope, and north-south component of the aspect) were derived from a digital elevation model with 25-m spatial resolution. Climate data (mean annual precipitation, temperature, and surface incoming shortwave radiation) were obtained using interpolated gridded monthly temperature, precipitation, and radiation data. All data were averaged over the time period 2000–2015.

Statistical Analysis. We tested effects of biodiversity on EVI_{GS}, $\overline{EVI}$, SOS, EOS, and GSL and the temporal trend and stability of these parameters using analysis of variance based on general linear mixed models, using R 3.3 (r-project.org) and ASReml (VSN International). Biodiversity and plot covariates were included as fixed effects and fitted sequentially. The spatial correlation among plots was

fitted as anisotropic exponential distance-decay of residual correlation. As plot covariates, we evaluated a total of 41 topographic and climatic indicators potentially related to vegetation activity. Variable selection was guided by redundancy analysis (RDA; https://cran.r-project.org/web/packages/vegan/index.html), allowing to pick representative variables with strong explanatory power from highly collinear sets. We finally settled on biogeographic region (BGR; factor with six levels) and altitude (continuous variable) because these terms integrate important climatic, topographic, and edaphic drivers and explained most variance. We determined their degree of confounding with biodiversity by fitting the biodiversity term before and after these covariates, i.e., we tested for (*i*) overall effects of biodiversity across regions and altitude and (*ii*) effects of biodiversity within biogeographic regions and constant altitude. We further determined 57 covariates characterizing land cover; these included the area of specific land cover types, land cover richness, and patch structure (e.g., largest patch, edge lengths, patch cohesion indices; ref. 52); we selected a subset of these using RDA, as described above, and included these in further models, together with a few climatic and topographic covariates we considered conceptually so important that we kept them, despite correlations with altitude and BGR (Tables S1 and S2). We quantified the relative importance of these covariates by calculating normalized effect sizes (Fisher's z transformation based on correlation coefficients derived from *F* ratios; ref. 19), with and without prior adjustments for the effect of altitude. Finally, we integrated the likely causal relationships among variables in a structural equation model (53). Starting from a saturated model, we removed nonsignificant paths with small path coefficients, until a model remained in which all path coefficients were significantly different from zero and for which there was no significant deviation between observed and model-implied covariance among the variables (χ^2 test; $P > 0.05$). These models were fitted by maximum likelihood, using the lavaan software (lavaan.ugent.be). Here, we focus on the most parsimonious of a wide array of models that we systematically explored. Additional models are provided as *SI Materials and Methods* (Table S1).

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Supporting Information

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SI Materials and Methods

Primary Productivity and Growing Season. EVI time series were downloaded for the years 2000–2015 and georeferenced to the Swiss CH1903+ grid. Data were then quality-filtered. We kept all MODIS EVI pixels that conformed to the following criteria:

i) Quality of EVI data product: We downloaded the MOD13Q1 product (18) in HDF format and filtered out low quality data by relying on the "VI usefulness information" coded in bits 2–5 of the MOD13Q1 "VI Quality Layer": We discarded all measurements with quality 8 (binary 1000_2) or worse.
ii) Minimum number of measurements per year: We filtered out pixels in years with less than 15 EVI measurements available after step *i*).
iii) Maximum noise in raw EVI data: We filtered out pixels where more than half of the original data points were replaced during the HANTS fitting process (47).
iv) Thresholds for LSP metrics: A minimum SOS was set to day 20 of the year, a maximum EOS was set to day 362. Pixels with SOS and EOS beyond these boundaries were discarded. Pixels with a mean EVI of 0.12 or lower were flagged as not vegetated and also discarded. Pixels with a growing-season EVI amplitude of 0.1 or less above the yearly mean were discarded as well because they did not allow a reliable determination of the growing season.

We then processed all data on a per pixel and year basis (years 2000–2015). Data were smoothed using a modified implementation of the HANTS algorithm (47). Our procedure was based on Fourier synthesis to estimate amplitudes and phase of three dominant frequencies for each MODIS pixel and year. Unlike standard fast Fourier transformation techniques, this algorithm also is applicable to unequally spaced data. Seasonal courses of EVI were fitted using a robust nonlinear procedure, adopting a Huber M-estimator that was used to iteratively reweigh data passed to a Levenberg–Marquard algorithm. As usual in the HANTS approach, the fit was repeated applying sequentially decreasing thresholds of 0.5, 0.2, 0.1, and 0.05 raw EVI values. Data with residuals exceeding these thresholds were replaced by model predictions. See Fig. 2 and *Methods* for the further processing and the derivation of GSL and productivity proxies.

Land Cover, Topography, and Climate: Description of Covariates and Sources. For each study plot, covariates related to land cover, topography, and climate were determined (selected covariates and respective times of collection and retrieval, spatial resolution, and data source are listed in Table S2). These specific covariates were selected based on a prior RDA (https://cran.r-project.org/web/packages/vegan/index.html), which helped to reduce colinearity. However, we also wanted keep important, interpretable, well-known drivers of ecosystem functioning in the dataset, despite their strong correlation (e.g., in the case of mean annual temperature and altitude). All data were averaged over the years 2000–2015.

Land-cover information was derived from point data with 100-m spatial resolution (product name: NOAS04) available from the Swiss Federal Statistical Office, GEOSTAT (https://www.bfs.admin.ch/bfs/de/home/dienstleistungen/geostat/geodaten-bundesstatistik/boden-nutzung-bedeckung-eignung/arealstatistik-schweiz/standardnomenklatur.html). We aggregated the original classification of 17 land-cover types into eight classes (forest, grassland, agricultural, urban, urban green, water, unproductive, bare land). From these data, we derived the fractional covers of each of the eight land-cover types. Land-cover richness was determined as the number of different land-cover types in each 1-km^2 study plot.

Topographic data (i.e., altitude, slope, and north-south component of the aspect; values averaged for the 1-km^2 plots) were derived from a digital elevation model (product name: DHM25) provided by the Swiss Federal Office of Topography (swisstopo; https://shop.swisstopo.admin.ch/en/products/height_models/dhm25).

Climate data (i.e., mean annual precipitation, temperature, and surface incoming shortwave radiation) were obtained using interpolated gridded monthly temperature, precipitation and radiation data; (product names: TabsM; RhiresM; msg.SIS.M) provided by the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss; a description of these data can be accessed under www.meteoswiss.admin.ch/content/dam/meteoswiss/de/service-und-publikationen/produkt/raeumliche-daten-temperatur/doc/ProdDoc_TabsM.pdf for temperature or www.meteoswiss.admin.ch/content/dam/meteoswiss/de/service-und-publikationen/produkt/raeumliche-daten-niederschlag/doc/ProdDoc_RhiresM.pdf for precipitation or www.meteoswiss.admin.ch/content/dam/meteoswiss/de/service-und-publikationen/produkt/raeumliche-daten-globalstrahlung/doc/ProdDoc_MSG.SIS.pdf for irradiation).

Data Subsets Excluding 1-Km^2 Plots with Agricultural Land or Deciduous Forest. To test whether results depended on the presence of agricultural land or deciduous vegetation in the 1-km^2 study plots, we created two data subsets where these land-cover types where excluded. Using these datasets, we repeated all analyses that we had performed with the full dataset ($n = 447$). Results are summarized in Figs. S2 and S3.

The first dataset ($n = 254$) contained only plots without any agricultural land. The second dataset ($n = 128$) contained only plots with at least 90% of the forested area classified as "evergreen" or "evergreen-mixed." We could not increase this threshold to 100% because only 14 plots containing "evergreen" or "evergreen-mixed" forest would have remained. The forest type classification was obtained from the Swiss Federal Statistical Office, GEOSTAT (https://www.bfs.admin.ch/bfs/de/home/dienstleistungen/geostat/geodaten-bundesstatistik/boden-nutzung-bedeckung-eignung/abgeleitete-und-andere-daten/waldmischungsgrad-schweiz.html; product name: Waldmischungsgrad der Schweiz; time of collection: 1990/92; spatial resolution: 25 m).

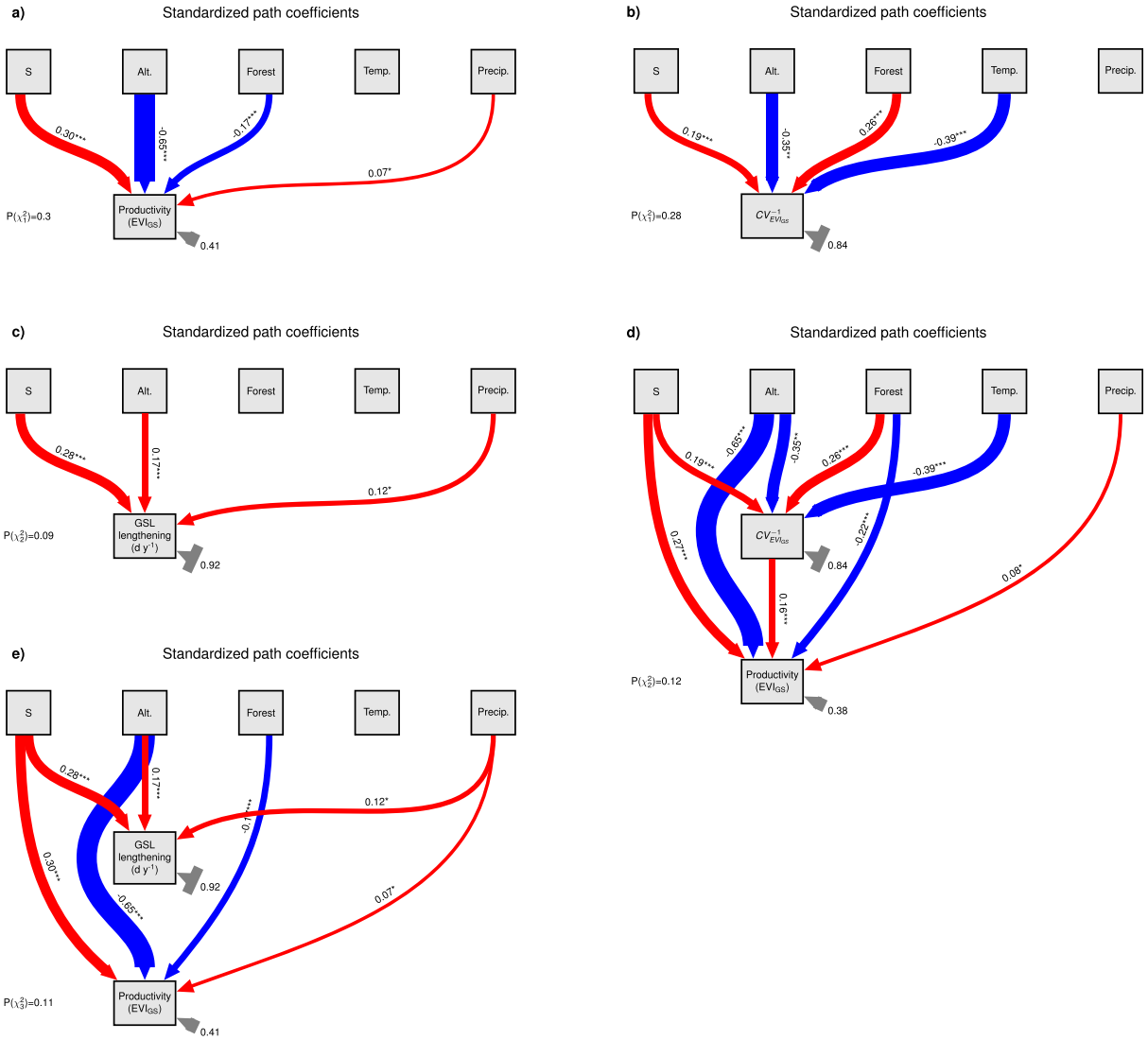

Fig. S1. Path diagrams showing effects of biodiversity (S) on 16-y average productivity (proxy: EVI_{GS}; *A*, *D*, and *E*), its temporal stability ($\mathbf{CV}^{-1}_{\mathbf{EVI_{GS}}}$; *B* and *D*) and the temporal trend of growing season lengthening (GSL lengthening; *C* and *E*). In addition to biodiversity, the structural equation models account for influences of altitude (Alt.) and variables related to land cover and climate. Only the standardized path coefficients are shown because the correlation of exogenous variables is described in Fig. 5*B*. Residual variances of the response variables are depicted with gray arrows ($n = 447$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; n.s., not significant). Forest, fraction of plot covered by forest; Precip., annual precipitation; Temp., mean annual temperature.

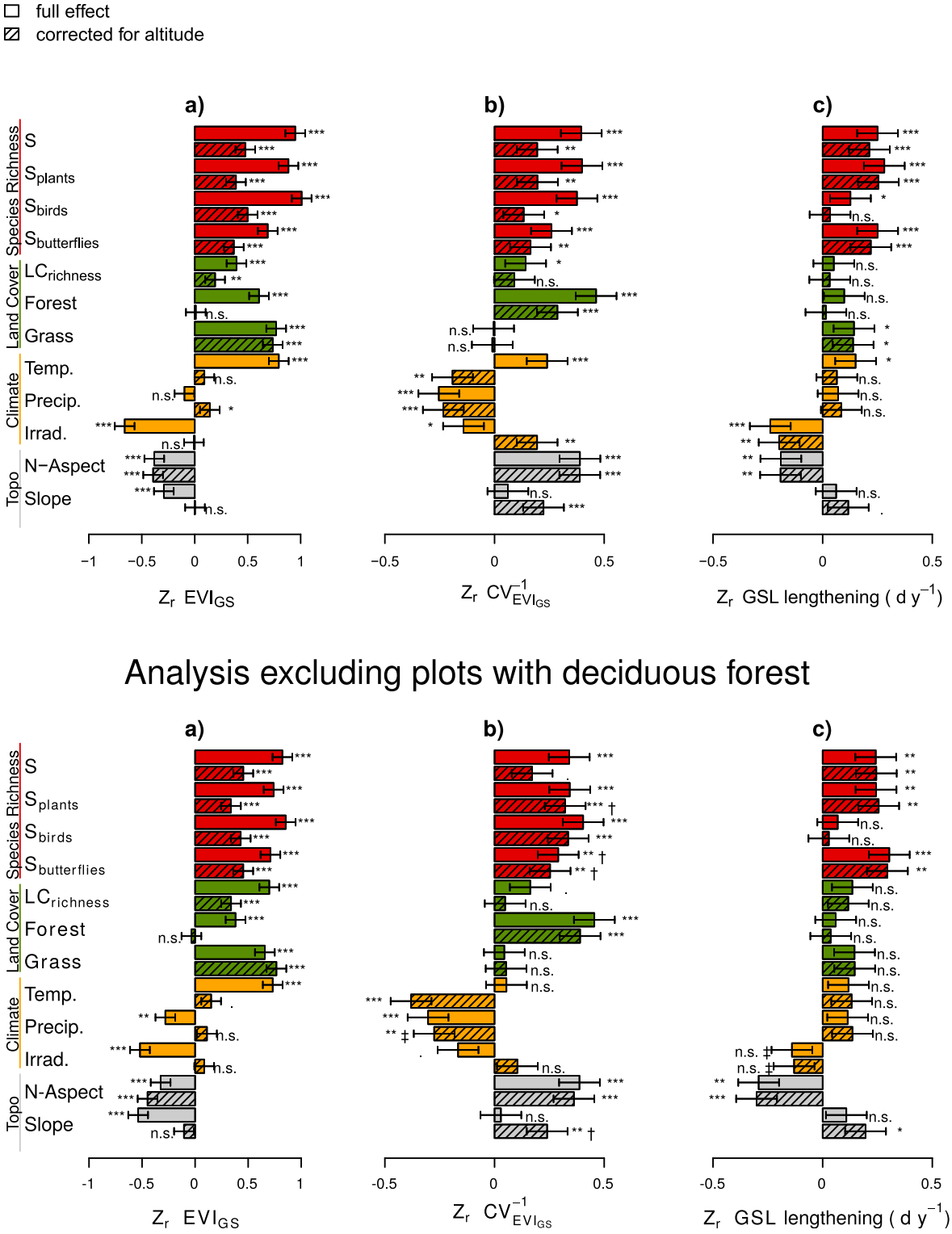

Fig. S2. Reanalysis of data subsets excluding agricultural land (*Upper*; $n = 254$) and deciduous forest (*Lower*; $n = 128$): Biodiversity effects on primary productivity (proxy: EVI_{GS}; *A*), its temporal stability ($CV^{-1}_{EVI_{GS}}$; *B*), and the temporal trend of growing season lengthening (GSL-lengthening, *C*) in the years 2000–2015. These results are very similar to the analysis of the full dataset (cf. Fig. 4). Effect sizes marked with † are derived from models with modeled isotropic (instead of anisotropic) spatial autocorrelation, whereas the ‡ symbol depicts effect sizes from models without considering the spatial autocorrelation. In these cases, models with anisotropic spatial autocorrelation did not converge. See Fig. 4 for further explanations.

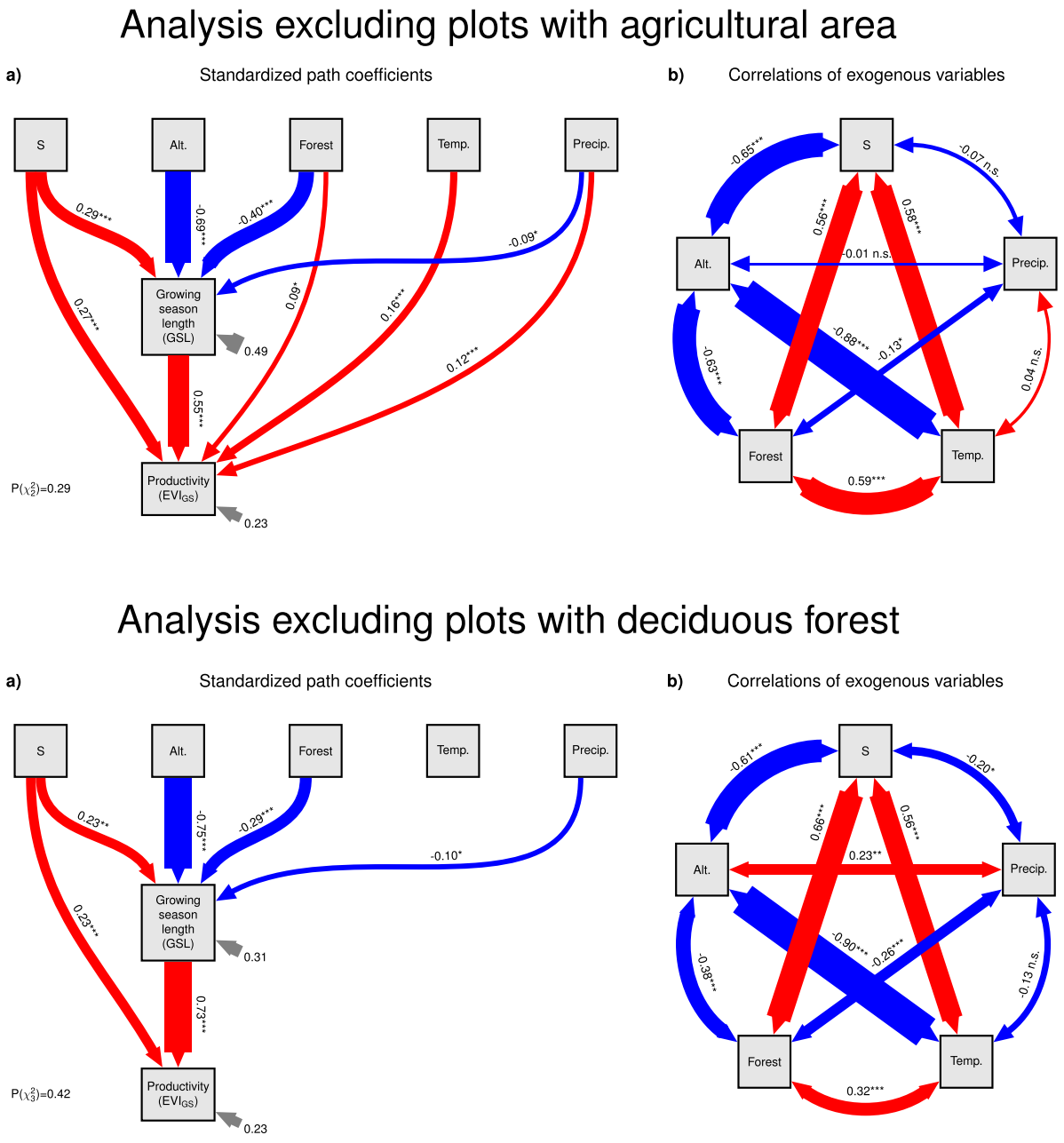

Fig. S3. Reanalysis of data subsets excluding agricultural land (*Upper*; n = 254) and deciduous forest (*Lower*; n = 128): Path diagrams showing effects of biodiversity on productivity (proxy: EVI_{GS}) that are mediated by or independent of changes in GSL. Besides biodiversity, the structural equation models account for influences of altitude (Alt.) and variables related to land cover and climate. The standardized path coefficients (*A*) and the correlation of exogenous variables (*B*) are shown separately. Gray arrows, residual variances of the response variables; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; Forest, fraction of plot covered by forest; n.s., not significant; Precip., annual precipitation; Temp., mean annual temperature. These results are very similar to the analysis of the full dataset (cf. Fig. 5).

Table S1. Effects of biodiversity (S and S_{plants}) on proxies of productivity (EVI_{GS}), the stability of productivity ($CV^{-1}_{EVI_{GS}}$), and GSL lengthening ($d{\cdot}y^{-1}$) when fitted after covariates related to climate, land cover, and topography

Model terms		S						S_{plants}					
		EVI_{GS}		$CV^{-1}_{EVI_{GS}}$		GSL lengthening, $d{\cdot}y^{-1}$		EVI_{GS}		$CV^{-1}_{EVI_{GS}}$		GSL lengthening, $d{\cdot}y^{-1}$	
BGR	Covariate	Effect size	Significance	Effect size	Significance	Effect size	Significance	Effect size*	Significance	Effect size*	Significance	Effect size*	Significance
—	—	0.25 ± 0.02	$F_{1,379} = 240$***	9.2 ± 1.4	$F_{1,445} = 45$***	1.1 ± 0.3	$F_{1,444} = 18$***	0.053 ± 0.004	$F_{1,378} = 172$***	2.1 ± 0.3	$F_{1,444} = 43$***	0.27 ± 0.06	$F_{1,442} = 19$***
	Alt.	0.15 ± 0.02	$F_{1,437} = 64$***	9.3 ± 1.6	$F_{1,438} = 35$***	1.6 ± 0.3	$F_{1,437} = 31$***	0.027 ± 0.005	$F_{1,437} = 32$***	2.2 ± 0.4	$F_{1,443} = 33$***	0.40 ± 0.07	$F_{1,441} = 34$***
	Slope	0.27 ± 0.02	$F_{1,402} = 278$***	9.1 ± 1.4	$F_{1,443} = 45$***	1.1 ± 0.3	$F_{1,443} = 17$***	0.059 ± 0.004	$F_{1,407} = 206$***	2.1 ± 0.3	$F_{1,443} = 43$***	0.26 ± 0.06	$F_{1,443} = 19$***
	N-Aspect	0.24 ± 0.02	$F_{1,375} = 220$***	11.0 ± 1.3	$F_{1,443} = 70$***	0.9 ± 0.3	$F_{1,443} = 13$***	0.050 ± 0.004	$F_{1,374} = 157$***	2.5 ± 0.3	$F_{1,442} = 65$***	0.24 ± 0.06	$F_{1,441} = 15$***
	Irrad.	0.23 ± 0.02	$F_{1,415} = 158$***	9.6 ± 1.5	$F_{1,443} = 41$***	1.2 ± 0.3	$F_{1,444} = 18$***	0.046 ± 0.005	$F_{1,410} = 103$***	2.2 ± 0.4	$F_{1,444} = 39$***	0.30 ± 0.07	$F_{1,442} = 20$***
	Precip.	0.25 ± 0.02	$F_{1,399} = 212$***	9.0 ± 1.4	$F_{1,443} = 42$***	1.2 ± 0.3	$F_{1,443} = 22$***	0.051 ± 0.004	$F_{1,395} = 151$***	2.0 ± 0.3	$F_{1,444} = 40$***	0.29 ± 0.06	$F_{1,443} = 23$***
	Temp.	0.18 ± 0.02	$F_{1,410} = 95$***	10.4 ± 1.5	$F_{1,442} = 45$***	1.4 ± 0.3	$F_{1,444} = 24$***	0.034 ± 0.005	$F_{1,409} = 55$***	2.4 ± 0.4	$F_{1,442} = 43$***	0.35 ± 0.7	$F_{1,444} = 26$***
	Grass	0.23 ± 0.02	$F_{1,376} = 237$***	8.7 ± 1.4	$F_{1,443} = 39$***	1.1 ± 0.3	$F_{1,442} = 17$***	0.050 ± 0.004	$F_{1,376} = 185$***	2.0 ± 0.3	$F_{1,443} = 39$***	0.26 ± 0.06	$F_{1,441} = 18$***
	Forest	0.29 ± 0.02	$F_{1,379} = 232$***	5.0 ± 1.5	$F_{1,441} = 11$**	0.8 ± 0.3	$F_{1,444} = 7$**	0.058 ± 0.005	$F_{1,381} = 157$***	1.2 ± 0.4	$F_{1,440} = 10$**	0.20 ± 0.07	$F_{1,443} = 9$**
	$LC_{richness}$	0.24 ± 0.02	$F_{1,380} = 178$***	10.4 ± 1.5	$F_{1,444} = 50$***	1.3 ± 0.3	$F_{1,442} = 22$***	0.048 ± 0.004	$F_{1,376} = 124$***	2.4 ± 0.3	$F_{1,443} = 47$***	0.31 ± 0.06	$F_{1,440} = 23$***
	Arable	0.26 ± 0.02	$F_{1,382} = 268$***	9.1 ± 1.4	$F_{1,443} = 45$***	1.1 ± 0.3	$F_{1,443} = 17$***	0.055 ± 0.004	$F_{1,383} = 195$***	2.1 ± 0.3	$F_{1,443} = 43$***	0.26 ± 0.06	$F_{1,442} = 19$***
	Urban	0.25 ± 0.02	$F_{1,376} = 241$***	9.5 ± 1.4	$F_{1,443} = 47$***	1.2 ± 0.3	$F_{1,443} = 21$***	0.054 ± 0.004	$F_{1,374} = 174$***	2.2 ± 0.3	$F_{1,441} = 47$***	0.30 ± 0.06	$F_{1,441} = 24$***
Yes	—	0.25 ± 0.02	$F_{1,387} = 236$***	9.5 ± 1.4	$F_{1,438} = 46$***	0.9 ± 0.3	$F_{1,438} = 13$***	0.053 ± 0.004	$F_{1,382} = 164$***	2.2 ± 0.3	$F_{1,434} = 45$***	0.24 ± 0.06	$F_{1,435} = 15$***
	Alt.	0.18 ± 0.02	$F_{1,416} = 78$***	7.2 ± 1.7	$F_{1,439} = 17$***	1.3 ± 0.3	$F_{1,438} = 18$***	0.031 ± 0.005	$F_{1,415} = 39$***	1.7 ± 0.4	$F_{1,438} = 17$***	0.33 ± 0.07	$F_{1,436} = 20$***
	Slope	0.27 ± 0.02	$F_{1,402} = 261$***	9.2 ± 1.4	$F_{1,437} = 44$***	0.9 ± 0.3	$F_{1,438} = 12$***	0.056 ± 0.004	$F_{1,400} = 184$***	2.2 ± 0.3	$F_{1,434} = 42$***	0.22 ± 0.06	$F_{1,436} = 14$***
	N-Aspect	0.24 ± 0.02	$F_{1,381} = 218$***	11.3 ± 1.3	$F_{1,437} = 71$***	0.8 ± 0.3	$F_{1,437} = 10$**	0.050 ± 0.004	$F_{1,376} = 152$***	2.6 ± 0.3	$F_{1,434} = 67$***	0.21 ± 0.06	$F_{1,434} = 12$***
	Irrad.	0.25 ± 0.02	$F_{1,422} = 185$***	8.6 ± 1.5	$F_{1,436} = 33$***	1.1 ± 0.3	$F_{1,434} = 16$***	0.050 ± 0.005	$F_{1,417} = 120$***	2.0 ± 0.4	$F_{1,439} = 32$***	0.28 ± 0.07	$F_{1,437} = 18$***
	Precip.	0.25 ± 0.02	$F_{1,398} = 212$***	8.8 ± 1.5	$F_{1,439} = 37$***	1.1 ± 0.3	$F_{1,438} = 15$***	0.052 ± 0.004	$F_{1,389} = 144$***	2.1 ± 0.3	$F_{1,436} = 36$***	0.26 ± 0.06	$F_{1,435} = 17$***
	Temp.	0.19 ± 0.02	$F_{1,394} = 108$***	9.8 ± 1.7	$F_{1,433} = 35$***	1.0 ± 0.3	$F_{1,437} = 11$***	0.037 ± 0.005	$F_{1,392} = 62$***	2.3 ± 0.4	$F_{1,428} = 34$***	0.26 ± 0.07	$F_{1,434} = 13$***
	Grass	0.23 ± 0.02	$F_{1,392} = 226$***	9.0 ± 1.4	$F_{1,437} = 40$***	1.0 ± 0.3	$F_{1,437} = 14$***	0.049 ± 0.004	$F_{1,390} = 171$***	2.2 ± 0.3	$F_{1,435} = 41$***	0.24 ± 0.06	$F_{1,434} = 15$***
	Forest	0.28 ± 0.02	$F_{1,383} = 224$***	5.3 ± 1.6	$F_{1,431} = 11$***	0.6 ± 0.3	$F_{1,438} = 5$*	0.057 ± 0.005	$F_{1,381} = 144$***	1.2 ± 0.4	$F_{1,426} = 11$***	0.17 ± 0.07	$F_{1,434} = 6$*
	$LC_{richness}$	0.24 ± 0.02	$F_{1,387} = 176$***	10.9 ± 1.5	$F_{1,435} = 51$***	1.1 ± 0.3	$F_{1,434} = 16$***	0.048 ± 0.005	$F_{1,377} = 117$***	2.5 ± 0.4	$F_{1,428} = 49$***	0.27 ± 0.07	$F_{1,428} = 17$***
	Arable	0.26 ± 0.02	$F_{1,386} = 262$***	9.3 ± 1.4	$F_{1,435} = 45$***	0.9 ± 0.3	$F_{1,437} = 13$***	0.054 ± 0.004	$F_{1,381} = 184$***	2.2 ± 0.3	$F_{1,432} = 44$***	0.23 ± 0.06	$F_{1,434} = 14$***
	Urban	0.26 ± 0.02	$F_{1,383} = 240$***	9.7 ± 1.4	$F_{1,435} = 47$***	1.0 ± 0.3	$F_{1,436} = 15$***	0.054 ± 0.004	$F_{1,377} = 170$***	2.3 ± 0.3	$F_{1,429} = 47$***	0.26 ± 0.06	$F_{1,431} = 18$***

Alt., mean plot altitude; BGR, the model does (yes) or does not (-) first account for effects of biogeographic region before the covariate; covariate, the specific covariate, which was included in the fixed-effects term before the biodiversity variables; effect size, coefficients (mean ± SE); Irrad., annual shortwave irradiation; $LC_{richness}$, number of land cover types in plot; N-aspect, North-south component of aspect; Precip., annual precipitation; S, the biodiversity index for all taxa combined; significance, *F* values with associated degrees of freedom and *P* values; Slope, average slope in degrees; S_{plants}, the biodiversity of plants; Temp., mean annual temperature; Forest, Grass, Urban, and Arable, fraction of plot covered by forest, grassland, urban, or arable land; for details see *SI Materials and Methods* and Table S2. ($n = 447$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; n.s. not significant).

*Effect size is given for an increase of 100 species.

Table S2. Covariates related to land cover, topography, and climate that were selected for the analysis presented in the main text

Category	Covariate	Time of collection	Time of retreival	Spatial resolution	Product name/source
Land cover	Grass (Fractional meadow/ Pasture cover) Forest (Fractional forest cover) $LC_{richness}$ (Number of different land-cover types)	2004–2009	January 10, 2016	100 m	NOAS04/Swiss Federal Statistical Office (FSO), GEOSTAT
Climate	Irradiation (SIS; Wm^{-2}; yearly mean)	2004–2012	November 26, 2016	0.0208 decimal degree (2.3 km West-East and 1.6 km South-North)	msg.SIS.M/Swiss Federal Office of Meteorology and Climatology (MeteoSwiss)
	Temperature (T; °C; yearly mean)	2000–2014			TabsM/Swiss Federal Office of Meteorology and Climatology (MeteoSwiss)
	Precipitation (P; mm; yearly sum)	2000–2014			RhiresM /Swiss Federal Office of Meteorology and Climatology (MeteoSwiss)
Topography	Altitude (m.a.s.l) Slope (°) N-Aspect: North-south component of the aspect (-1 if south-exposed; 1 if north-exposed)	1978–2001	May 22, 2016	25 m	DHM25/Swiss Federal Office of Topography (swisstopo)

General Discussion

Synthesis

Biodiversity effects are relatively context-independent

The proposition that biodiversity effects depend on environmental conditions because these affect mechanisms of coexistence is reasonable (Leibold *et al.* 2017). Mechanisms of coexistence (i.e. causes of biodiversity) affect the composition, the interaction, the shape, and the distribution of traits and species, which in turn determine ecosystem patterns and processes (Duflot *et al.* 2014; Gamez-Virues *et al.* 2015; Perovic *et al.* 2015; Brose & Hillebrand 2016; Fournier *et al.* 2017; Leibold *et al.* 2017).

Many studies in non-experimental conditions across different ecosystem types have found context-dependent B-EF relationships (Paquette & Messier 2011; Vilà *et al.* 2013; Allan *et al.* 2015; Jing *et al.* 2015; Wu *et al.* 2015; Jucker *et al.* 2016; Liang *et al.* 2016; Ratcliffe *et al.* 2016; Jactel *et al.* 2017; Ratcliffe *et al.* 2017). However, it generally has been difficult to attribute this context-dependency unequivocally to either causes or effects of biodiversity (Grace 1999; Gillman & Wright 2006; Grace *et al.* 2007; Cardinale *et al.* 2009; Grace *et al.* 2016; Mori 2018). A few studies experimentally investigated the context-dependence of biodiversity effects and found mixed results for ecosystem productivity and stability (Fridley 2002; Hautier *et al.* 2014; Hautier *et al.* 2015; Craven *et al.* 2016).

The findings in this thesis do not support the idea that biodiversity effects strongly depend on the environmental context. Quite on the contrary, in all three chapters the positive biodiversity effects on ecosystem functions were very robust and consistent across various environmental conditions prevailing in different biogeographic regions, altitude ranges and ecosystem types. The fact that I found positive, consistent, diversity – functioning relationships for local (α-), regional (γ-), and spatial (β-) diversity corroborates the notion that diversity effects on the functioning and stability of complex systems are a general phenomenon and independent of specific scales of space, time or ecological organization.

The finding that biodiversity effects are rather general is in line with early theoretical considerations (Macarthur 1955; Hutchinson 1959) and with conclusions from small-scale experiments (Schmid & Hector 2004). Nevertheless, this finding is remarkable because certain underlying mechanisms of biodiversity effects, such as complementarity and

selection effects, can depend on context (Fargione *et al.* 2007; Mori 2018). It has additionally been shown that increased complementarity effects can lead to increased net biodiversity effects in experimental conditions (Zuppinger-Dingley *et al.* 2014). Therefore, context-dependence of complementarity effects could drive context-dependence of net biodiversity effects also in real-world conditions.

In the real-world conditions covered by my studies, I found only a few cases that could demonstrate an indication of the context-dependence of net biodiversity effects: for example, in chapter 3, I found that effects of plant γ-diversity (but not effects of multi-taxon γ-diversity) significantly decreased with increasing landscape diversity (Fig.1). However, this result could equally well be interpreted as plant γ-diversity effects that are partially masked by landscape diversity, similarly as has been found in agricultural systems (Batary *et al.* 2010; Tscharntke *et al.* 2012; Gamez-Virues *et al.* 2015; Baillod *et al.* 2017).

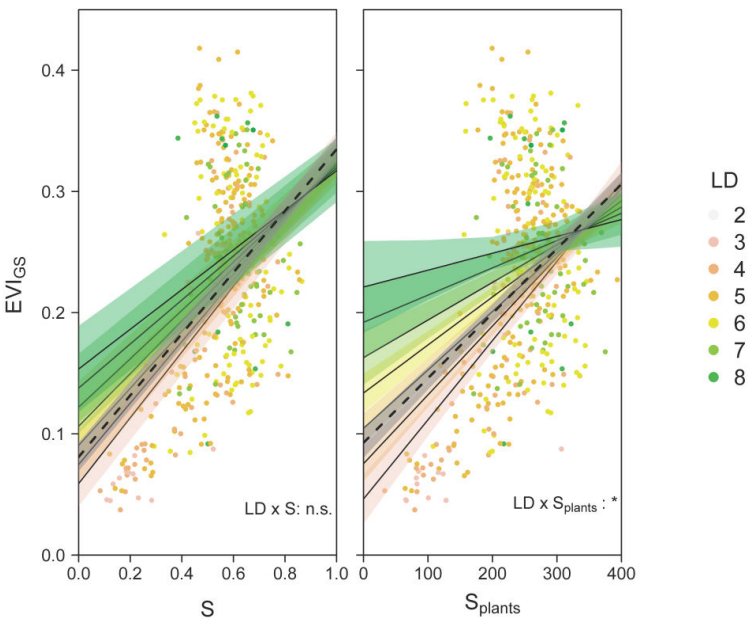

Fig.1 Effects of γ-diversity (multi-taxon diversity: S; vascular plant diversity: S_{plants}) on yearly landscape-scale primary productivity averaged in the time 2000-2015 (EVI_{GS}; N=447; cf. chapter 3, biodiversitymonitoring.ch). Whereas S effects (left panel) are independent of landscape diversity (LD; LD × S interaction term: 'n.s.':P≥0.1), S_{plants} effects significantly decrease with increasing levels of LD (LD × S_{plants} interaction term: '*':P<0.05; right panel). Solid, colored lines: Model predictions for specific levels of LD, shaded areas: Predictions' standard errors of the mean, dashed lines: Overall biodiversity effects.

Also, in chapter 3, plant γ-diversity (but not effects of multi-taxon γ-diversity) effects showed an insignificant tendency to decrease with lower altitudes (cf. chapter 3; Oehri *et al.* 2017), which comprise large parts of the Central Plateau with higher nutrient availability

in Switzerland (Rihm 1996 ; Fig.2). This finding indicates that plant γ-diversity effects might have decreased because of decreasing complementarity effects with higher nutrient availability (Grime 1973, 1979; Huston 1979; Huston 2014).

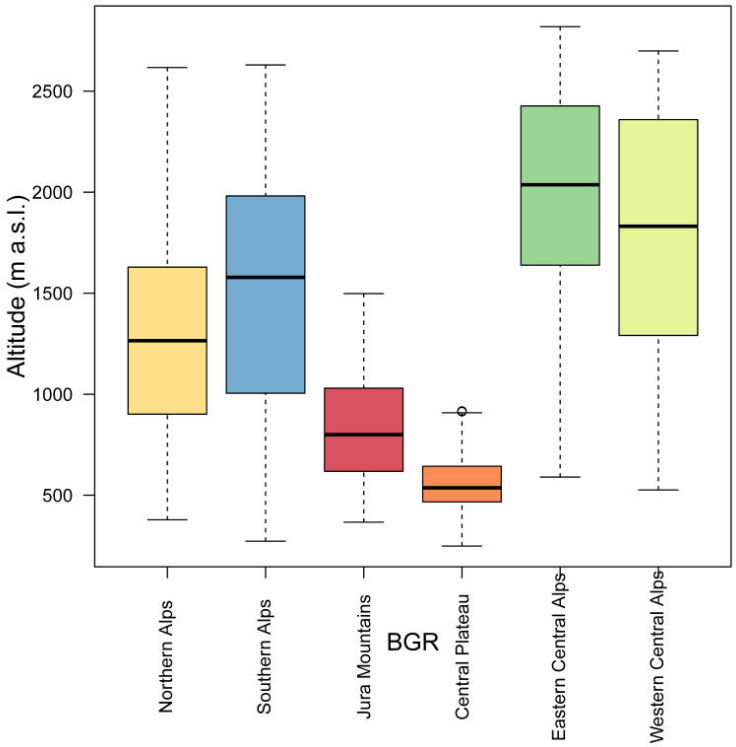

Fig.2. Altitude distribution of the 1km^2 plots studied in chapter 3 grouped by the six different biogeographic regions (BGR) of Switzerland (cf. chapter 3). Northern Alps: 378 – 2,617 m; Southern Alps: 273-2,630 m; Jura Mountains: 366-1,498 m; Central Plateau: 248-917 m; Eastern Central Alps: 590 – 2,818 m; Western Central Alps: 526 –

Therefore, I cannot completely exclude that biodiversity effects are context-dependent. However, because the gradients in environmental conditions covered by my studies were relatively large, I consider it unlikely that I missed the conditions needed to detect significant context-dependencies of diversity effects.

I argue that biodiversity effects can be context-independent because biodiversity effects emerge via a variety of different mechanisms (cf. Hooper *et al.* 2005; Cardinale *et al.* 2012; Loreau & de Mazancourt 2013; Tilman *et al.* 2014; Isbell *et al.* 2018). For example, biodiversity effects can emerge via species complementarity effects (Hooper *et al.* 2005), positive species interactions (cf. 'facilitation', Wright *et al.* 2017), sampling effects (i.e. 'positive selection' effects, Loreau & Hector 2001), and spatially or temporally desynchronized species population dynamics (cf. 'portfolio effects', Schindler *et al.* 2015 ;

'spatial insurance effects', Loreau *et al.* 2003a ; 'temporal insurance', Yachi & Loreau 1999; Allan *et al.* 2011).

It could be that these mechanisms compensate each other or average out under different environmental conditions. The exact mechanisms that drive biodiversity effects and their context-dependence are not well understood and need to be addressed in future research that is able to account simultaneously for causes and effects of biodiversity in complex, real-world conditions. So far, I found a robust pattern of positive biodiversity effects on ecosystem functions, despite that the manifold underlying mechanisms may be context-dependent.

Biodiversity effects are of major importance

In accordance with previous findings from small-scale experiments (Hooper *et al.* 2012; Tilman *et al.* 2012) and recent evidence at larger spatial scales (Maestre *et al.* 2012; Duffy *et al.* 2017), I found that biodiversity is equally or even more important than other environmental drivers for ecosystem functions and ecosystem stability in real-world landscapes. In chapter 1, local tree diversity (α-diversity) ranged among the most important predictors of forest productivity and growing season length compared with a variety of predictors characterizing stand structure, landscape structure, topography and climate. Similarly, in chapter 3, the magnitude of γ-diversity effects was comparable or even larger than the magnitude of effects of climate, land-cover and topography. In this chapter, I also found that environmental drivers and γ-diversity are strongly correlated among each other and effects of environmental drivers were partially mediated via γ-diversity. This result is in accordance with previous findings at smaller spatial scales (Isbell *et al.* 2013; Allan *et al.* 2015; Hautier *et al.* 2015). The γ-diversity effects I found in chapter 3 were also slightly larger in magnitude than biodiversity effects identified in experiments (Balvanera *et al.* 2006; Schmid *et al.* 2009), which is exactly what has been found by a recent study, that predominantly covered α-diversity effects (Duffy *et al.* 2017).

Hence, in contrast to the assumptions of minor importance of biodiversity (Srivastava & Vellend 2005; Grace *et al.* 2007; Hillebrand & Matthiessen 2009), I found that biodiversity effects are of major importance to the functioning and stability of real-world landscapes.

Biodiversity affects vegetation phenology and climate stability

In all three chapters I found that the diversity of species and ecosystem types is of major importance for average vegetation productivity at the local and landscape-scale. In chapter 2 and 3 I found that β- and γ-diversity increase the temporal stability of productivity.

Additionally, I found that the diversity of species and ecosystem types affects further ecosystem functions, such as vegetation phenology, which has rarely been explored in biodiversity studies to date (but see: (Rathcke & Lacey 1985; Hooper 1998). In chapter 3, I detected a general change of vegetation phenology across Switzerland during the study period of 2000-2015. Specifically, the yearly growing season length increased with time, so that the average growing season length today is longer than 15 years ago. This is a globally observed phenomenon attributed to climate warming (Menzel 2013; Garonna *et al.* 2014). Landscapes with higher γ-diversity exhibited significantly accelerated growing season lengthening. This finding suggests that landscapes with higher regional biodiversity can more quickly and more efficiently adapt to changing environmental conditions (Hutchinson 1959; Hutchinson 1978). The ability to phenologically adapt to changing environmental conditions, referred to as 'phenological sensitivity', contributes to the long-term survival of species (Jump & Penuelas 2005; Cleland *et al.* 2012). Therefore, I argue that γ-diversity can determine the resilience of real-world landscapes faced with global change. In chapter 1, local tree diversity (α-diversity) was positively related to the average growing season length of the studied forest stands, but the study period (2 years) was too short to detect changes in a lengthening trend, as I did in chapter 3. In chapter 2, the study period was similar as in chapter 3 (years 2000-2016) but I did not find landscape diversity (β-diversity) effects on growing season lengthening trend. Instead, β-diversity increased the average yearly growing season length and the temporal stability of growing season length in the 250,000 m^2 landscapes I investigated. In both chapter 2 and 3, β- and γ-diversity effects were mediated via the start of vegetation activity in spring ('start of season'), but not via the decline of vegetation activity in autumn ('end of season'), suggesting that start and end of season are governed by different mechanisms (Gallinat *et al.* 2015).

Importantly, α-, β- and γ-diversity effects on vegetation productivity and phenology can contribute to further ecosystem functions relevant in real-world landscapes, such as

climate regulation. The positive effects of α-, β- and γ-diversity on vegetation productivity, growing season length, and the temporal stability of these variables could critically impact the biogeochemical fluxes of water and carbon, for example (McPherson 2007; Bonan 2008). In chapter 2 I found that β-diversity is additionally linked to an increased overyielding (Tilman 1999; Schmid *et al.* 2008) and an increased stability of summer land-surface albedo in the near-infrared domain. Therefore, β-diversity could critically contribute to climate regulation not only via changes in biogeochemical fluxes but also via changes in biophysical landscape properties (Claussen *et al.* 2001; Oke 2002; Bright *et al.* 2015; Devaraju *et al.* 2015; Zeng *et al.* 2017). These findings suggest that β- and γ-diversity likely contribute to regional climatic stability via increased stability in vegetation productivity, phenology, and summer near-infrared albedo.

Thus, I highlight that biodiversity affects hitherto underexplored ecosystem functions, such as phenological sensitivity and climate stability, which can contribute to the resilience of real-world landscapes (Fig.3).

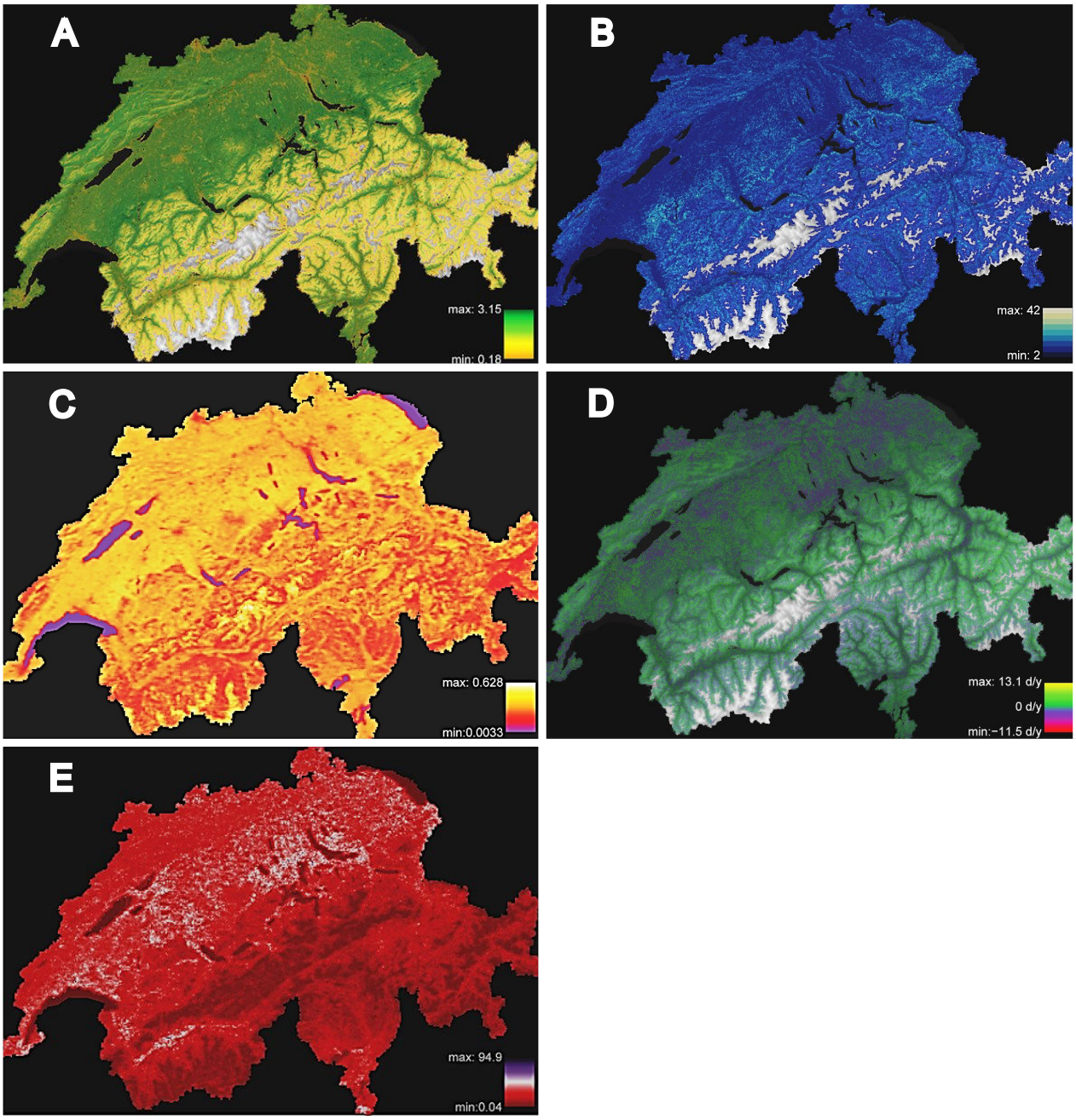

Fig.3 Examples of satellite-derived ecosystem functions investigated in this thesis. Measures were derived from MODIS Enhanced Vegetation Index (EVI; (Didan 2015); A,B,D) or MODIS albedo products (Schaaf & Wan 2015 ; C,E) in the time of 2000-2016 and approximate **A**: yearly primary productivity (integrated growing season EVI, cf. chapter 3), **B**: inter-annual stability of yearly primary productivity, **C**: summer near-infrared albedo, **D**: growing season lengthening (cf. chapter 3), and **E:** inter-annual stability of summer near infrared albedo.

Biodiversity effects are similar for α-, β-, and γ-diversity

In this thesis I measured biodiversity at two scales of space: the local (≤ 950 m^2; chapter 1) and the landscape scale (62,500m^2 - 1,000,000 m^2; chapter 3). I broadly focused on two scales of time: the study in chapter 1 covers two years, whereas the studies in chapter 2 and 3 cover 17 and 16 years, respectively. I also measured biodiversity at two scales of ecological organization (Jorgensen & Nielsen 2013): at the scale of species (α- and γ- diversity; chapter 1 and 3), and at the scale of whole ecosystems (β-diversity; chapter 2).

While ecosystems jointly refer to species assemblages together with their abiotic environment, β-diversity usually refers to species assemblages only (Whittaker 1972; Anderson *et al.* 2011; Socolar *et al.* 2016). However, I argue that the spatial diversity of ecosystem types necessarily reflects the spatial turnover of species that compose these ecosystem types (Chapin *et al.* 2002). Therefore, I use the term β-diversity, even though I refer to land-cover type diversity derived from geographic information in chapter 2.

Comparing β-diversity effects across scales, I found that β-diversity effect sizes were consistently (although not always significantly) larger in landscapes with a larger area (250,000m^2) compared to landscapes with a smaller area (62,500m^2; cf. chapter 2). I additionally found that β-diversity only affected ecosystem functions measured at the landscape scale (chapter 2) and was not directly related to ecosystem functions at the local scale (chapter 1). These results indicate that β-diversity effects on ecosystem functions are more pronounced at larger spatial scales. Nevertheless, β-diversity was positively related to α-diversity (chapter 1) and γ-diversity (chapter 3; Fig. 4), which suggests that β-diversity could contribute to ecosystem functions at smaller spatial scales via the promotion of species diversity and consequent spatial insurance effects (Loreau *et al.* 2003a; Tscharntke *et al.* 2012).

I found striking similarities among α-, β- and γ- diversity effects. I deliberately derived comparable measures of ecosystem functions at local and landscape spatial scales, i.e. vegetation productivity and growing season length. All detected α-, β- and γ- diversity effects on productivity and growing season length were positive and consistent across various types of environmental conditions. Both γ- and β-diversity were consistently related to increased temporal stability of productivity. I could not test α-diversity effects on ecosystem stability because the duration of the study was too short (2 years). In chapter 2

I found that β-diversity can affect the stability of land surface properties relevant for climate regulation, such as the near-infrared land surface albedo.

To compare the α-, β-, and γ-diversity effects on vegetation productivity (LAI in chapter 1, EVI_{GS} in chapter 2 and 3), I recalculated meta-analytic effect sizes from correlation coefficients derived from F-ratios (Zr; (Rosenthal 1994), as described in chapter 2 and 3). I calculated these Zr values for effects of α-, β-, and γ-diversity in models as described in chapters 1, 2, and 3 respectively, except that I adjusted for biogeographic region and altitude in the models before testing α- and γ-diversity effects, in order to make them comparable to the β-diversity effects that were adjusted for these variables by default. I found that the Zr of α-, and γ- diversity were very similar ($Zr_{\alpha\text{-div}}$: 0.45; $Zr_{\gamma\text{-div}}$: 0.42). Also the β-diversity effect sizes were similar in magnitude for landscapes with 500m extent ($Zr_{\beta\text{-div}}$: 0.38) and only decreased for landscapes with 250m extent ($Zr_{\beta\text{-div}}$: 0.28).

These results represent among the first empirical evidence (but see: Aragon *et al.* 2011; van der Plas *et al.* 2016) supporting the importance of α-, β-, and γ-diversity for the functioning and stability of real-world landscapes. These findings are in line with theoretical predictions (Loreau *et al.* 2003a; Wang & Loreau 2014; Wang & Loreau 2016) and evidence from studies in experimental conditions at smaller spatial scales (Pasari *et al.* 2013; Alsterberg *et al.* 2017; Hautier *et al.* 2018).

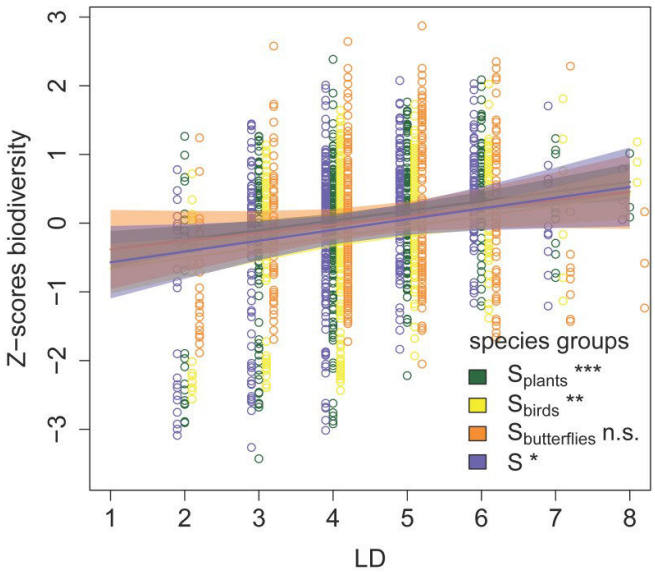

Fig.4 Predicted landscape diversity effects (LD; i.e. Land-cover type richness in 447 1 km^2 landscapes across Switzerland, cf. chapter 3) are positive for Z-scores of regional biodiversity, but differ in significance ('***':P<0.001; '**': P<0.01, '*': P<0.05; '.': P<0.1; 'n.s.':P≥0.1). LD effects (solid lines) and corresponding standard error of the means (shaded areas) are predicted at a mean altitude of 1,180 m a.s.l. and are adjusted for biogeographic region. S_{plants}: vascular plant species richness, S_{birds}: breeding bird species richness, $S_{butterflies}$: butterfly species richness, S: multi-taxon species richness (cf. chapter 3,

What can we know? - Limitations

The primary focus of this thesis was to investigate biodiversity effects on ecosystem functions across scales in real-world landscapes, where ecosystem functions actually underpin ecosystem services and human-wellbeing (Cardinale *et al.* 2012; Isbell *et al.* 2017). I took advantage of sophisticated technology, high computational power and the availability of large amounts of environmental data to systematically assess real-world biodiversity-ecosystem functioning (B-EF) relationships. I found patterns that are only consistent with a theory in which biodiversity is a major driver of ecosystem functions and stability.

Nevertheless, the observational character of the analyses in all three chapters entails the disadvantage that the specific mechanisms behind observed patterns cannot be inferred with certainty.

In chapter 3, I derived γ-diversity from species presence data, with no information on abundance or species trait values. I also could not attribute the landscape-level productivity measured by satellite-remote sensing to contributions of specific species. Similarly, in chapter 1, I did not consider species abundance or species traits. Hence, I could not infer if the observed α-diversity and γ-diversity effects were due to species complementarity, sampling effects, or desynchronized population dynamics, for example (Hooper *et al.* 2005; Loreau & de Mazancourt 2013). Because of similar reasons, in chapter 3, I could not resolve why γ-diversity affected the timing of start of season, but not the end of season (Gallinat *et al.* 2015).

In chapter 2, I also could not confidently infer the mechanisms behind observed β-diversity effects on landscape functions and stability. Similarly as in chapter 3, I could not determine which land-cover types contributed how much to the remotely-sensed productivity that was measured at the landscape-scale. I also could not completely determine if land-cover type diversity effects were ultimately mediated via γ-diversity, because I did not have species diversity data for these landscapes at hand. Additionally, I could not disentangle if it was mainly the compositional or the configurational (Duelli 1997; Fahrig *et al.* 2011; Pasher *et al.* 2013) diversity of land-cover types that mediated the positive effects on landscape functions and stability, because we did not balance land-cover (i.e. compositional) diversity with configurational diversity. In contrast to findings in experimental B-EF studies (Tilman *et al.* 2014), landscape diversity effects were not as

pronounced at low levels of diversity compared to high levels of diversity. Therefore, the mechanisms governing β-diversity effects likely differ from mechanisms of α-diversity effects and could involve complex higher order interactions among ecosystem types, similar as the ones found among species (Levine *et al.* 2017).

Hence, the investigations in this thesis were largely focused on patterns in realistic conditions, often at the expense of finding specific mechanisms governing these patterns (cf. also the trade-off among realism, precision and generality; Levins 1966).

By virtue of advanced computational techniques and large amounts of available data, I could statistically control for multiple correlations among biodiversity and environmental factors that would otherwise have biased the estimates of biodiversity effects. However, I want to highlight that there also exist inherent correlations among phenomena that cannot completely be disentangled, not only in real-world conditions but also when theoretically considered: For example, habitat amount and habitat diversity in a landscape are inherently correlated, because a higher number of habitats necessarily entails smaller areas of each habitat type in any equally sized area (Fahrig 2017). Also is any habitat with a large amount of area more likely to exhibit a higher habitat connectivity (Fahrig 2017). Similarly, the compositional diversity of a landscape is intrinsically correlated to its configurational diversity, so that landscapes with only few habitat types have limited potential configurations compared to landscapes with many habitat types (Duelli 1997; Fahrig *et al.* 2011; Pasher *et al.* 2013). Additionally, in chapter 2, I found that an increased primary productivity affecting the carbon balance intrinsically entails increased values of near-infrared surface albedo and hence, changes in the surface energy balance. I argue that such inherent correlations need further attention if we want to understand biodiversity effects on the function and stability of real-world landscapes.

What ought we to do? - Future directions

The findings of this thesis support the notion that biodiversity is essential for the functioning and stability of real-world landscapes that sustain human well-being. I found that biodiversity effects are of substantial magnitude and consistent across environmental conditions. Biodiversity effects are also consistent across scales of ecological organization: Not only local and regional species diversity (i.e. α- and γ- diversity) sustain landscape functions and stability, but also spatial dissimilarity among ecosystem types (i.e. β-diversity). These findings highlight the potentially large, dire consequences for human well-being via both species extinctions (Pimm *et al.* 2014; Ceballos *et al.* 2015) and landscape simplification (McKinney & Lockwood 1999; Olden & Rooney 2006; Baiser *et al.* 2012).

Because we still have a lack of knowledge on the specific mechanisms that govern biodiversity-functioning relationships in real-world landscapes, our ability to predict specific consequences of biodiversity loss and to supply recommendations helping to prioritize specific land management plans remains limited. Therefore, more in-depth analyses, which can disentangle specific mechanisms behind B-EF relationships in complex real-world landscapes, are needed.

Firstly, we need to discriminate mechanisms of species coexistence from biodiversity effects and elucidate how they change with environmental conditions (Gross & Cardinale 2007; Brose & Hillebrand 2016; Mori 2018). Based on the large body of research and the analyses presented in this thesis, I confidently argue that biodiversity is both an emergent property and a major force affecting ecosystems in real-world landscapes. The discrimination of causes and effects of biodiversity is crucial (Mori 2018): the understanding of the causes can inform about conditions leading to changes in biodiversity. However, only the understanding of the effects can inform about the consequences of biodiversity loss for ecosystem functioning, services and eventually, the human existence.

Secondly, and related to the first statement, we need to better understand the specific mechanisms governing biodiversity effects, such as complementarity, facilitation, selection and species asynchrony (Loreau & de Mazancourt 2013; Tilman *et al.* 2014). We also need to know how these mechanisms are affected by environmental conditions and how changes in these mechanisms can affect the magnitude of net biodiversity effects (Isbell *et*

al. 2018). To find mechanisms that govern diversity effects at the species level, we need information not only on the presence, but also on the abundance, the distribution and the functional trait values of these species (Violle *et al.* 2007). To find mechanisms that govern diversity effects at the ecosystem level, we ideally combine species information with ecosystem type information, to estimate the fraction of ecosystem diversity effects mediated primarily by regional or local species diversity. Also, collecting information on structures and processes in specific ecosystem types present in a landscape could allow to investigate if mechanisms such as complementarity play a role not only among species, but also among ecosystem types (Alsterberg *et al.* 2017). It is also crucial to disentangle effects of compositional and configurational diversity to understand ecosystem diversity effects (Duelli 1997; Fahrig *et al.* 2011; Pasher *et al.* 2013).

Finally, I highlight the importance of accounting for hitherto underexplored ecosystem functions relevant for landscape-level ecosystem services to humans, such as vegetation phenology and climate regulation. In future studies, it should be considered that ecosystems can influence the carbon, surface energy and water budgets not only via primary productivity, but also via changes in surface properties such as albedo or roughness length (Oke 2002; McPherson 2007; Mahmood *et al.* 2014). It has been found that landscape diversity can affect temperature, precipitation and wind shear patterns (Laurance *et al.* 2011; Pielke *et al.* 2011) and I highlight that the relevance of biodiversity for human well-being might be underestimated if we do not consider such important functions.

I argue that the application of a systematic study design in real-world conditions as I did in chapter 2 represents a valuable approach to tackle these remaining challenges. Such ‘quasi experimental’ approaches are successfully applied in other fields of science (Ferraro & Hanauer 2014). The current surge in computational power and the availability of large amounts of environmental data could propel the ability of this approach to yield precise information on specific mechanisms, while still focusing on complex, realistic conditions. For example, in addition to what I did in chapter 2, ‘landscape plots’ could be selected with respect to balanced and orthogonal gradients in compositional and configurational landscape diversity, habitat amount, connectedness, and species diversity.

Very importantly, such an approach needs to be guided by appropriate, integrative theoretical frameworks that simultaneously account for causes and consequences of

biodiversity, for interactions with environmental context and for multi-trophic interactions among species and ecosystems. Such frameworks can guide the proper, targeted design of studies and additionally yield important null-models that allow for comparing expected with observed patterns. Such integrative frameworks are recently being established (Loreau *et al.* 2003b; Gross & Cardinale 2007; Massol *et al.* 2011; Grace *et al.* 2016; Fournier *et al.* 2017; Leibold *et al.* 2017; Letten *et al.* 2017; Barnes *et al.* 2018; Godoy *et al.* 2018) and now need to be applied in studies that focus on B-EF relationships in complex, real-world conditions at large spatial scales.

What may we hope? - Conclusions

In this thesis, I made use of increasingly available technological advancements to systematically investigate biodiversity effects on the biosphere's structures and processes at large scales of space, time and ecological organization. I found empirical evidence that biodiversity is of a general and major importance for the functioning and the resilience of real-world landscapes. Therefore, my findings support the framework established in more than 25 years of B-EF research focusing on small-scale experiments (Cardinale *et al.* 2012; Tilman *et al.* 2014). My findings contribute to resolving current debates (Lepš 2004; Srivastava & Vellend 2005; Thompson & Starzomski 2007; Duffy 2009; Brose & Hillebrand 2016; Wardle 2016) and highlight the relevance of biodiversity for sustaining the human existence.

I conclude that the drastic biodiversity loss and landscape simplification in the Anthropocene pose a serious threat to human well-being.

We therefore may hope that humans do not become what has long been called a mere hypothetical monster: A 'Darwinian Demon' (Law 1979) that eventually outcompetes all other species sharing its space and time.

We may hope that we humans can change our ethics and behavior in such a way that the diversity of life does not vanish before we had the chance to truly understand and appreciate its fascination and importance for our and future lives of any kind.

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Curriculum Vitae

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Education

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Ph.D. program: Ecology
The Ph.D. thesis was carried out within the framework of the University Research Priority Programme Global Change and Biodiversity (URPP GCB) at the Departement of Evolutionary Biology and Environmental Studies at the University of Zurich, CH.
Project PI‘s and Supervisors: Prof. Dr. Pascal A. Niklaus and Dr. Gabriela Schaepman-Strub. Co-Supervisor: Prof. Dr. Bernhard Schmid

2012-2014: Master of Science in Environmental Sciences at the University of Zurich, CH (90 ECTS). Thesis title: Investigating the relationships among biodiversity, land use and ecosystem services: Selection and comparative analysis of specific terrestrial sites in Switzerland.
Supervisor: Prof. Dr. Bernhard Schmid

2009-2012: Bachelor of Science in biology (180 ECTS) at the University of Fribourg, CH, with a major in biology (120 ECTS) & minors in geography and in environmental sciences, 30 ECTS, each. Thesis title: Verification of a NPA binding pocket in TWISTED DWARF1. Supervisor: Prof. Dr. Markus Geisler

2002-2008: Eidgenössische Matura, Typus M, Schwerpunkt: Bildnerisches Gestalten, Kantonsschule Zug, CH

Publications

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2017). Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. *Proceedings of the National Academy of Sciences*, *114*(38), 10160-10165.

Zhu, J., Zwiewka, M., Sovero, V., di Donato, M., Ge, P., **Oehri, J.**, (...), & Geisler, M. (2016). TWISTED DWARF1 mediates the action of auxin transport inhibitors on actin cytoskeleton dynamics. *The Plant Cell Online*, tpc-00726.

Conference contributions

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2016). The role of diversity in real-world ecosystem functioning: Insights from investigations at the landscape scale. Oral presentation at the Ecological Society of America (ESA) Annual Meeting 2016 (07.08.-12.08.2016) in Fort Lauderdale, FL, USA

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2016). Biodiversity effects on ecosystem functioning and the energy cycle – from the plot to the landscape scale. Oral poster presentation at the University Research Priority Programme Global Change and Biodiversity (URPP GCB) conference (28.08.-01.09.2016) in Ascona, Switzerand.

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2017). Landscape diversity promotes primary productivity and summer climate stability across large spatial scales
Oral poster presentation at the British Ecological Society (BES) Annual Meeting 2017 (11.12.-14.12.2017) in Ghent, Belgium

Research Seminars

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Oral presentation in the internal BEEES Seminar of the Department of Evolutionary Biology and Environmental Studies at the University of Zurich (14.04.2015). Host: Prof. Dr. Pascal A. Niklaus

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2016). Biodiversity and ecosystem functioning at the landscape scale.
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Teaching activities

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2014, 2015:	Function: teaching assisstant UWW 252 Spatial ecology and remote sensing, lectures and practical course Responsible: Dr. Gabriela Schaepman-Strub Location: University of Zurich
2016, 2017:	Function: lecture preparation and substitution UWW 251 Global change and ecosystem ecology, lectures Responsible: Prof. Dr. Pascal A. Niklaus Location: University of Zurich
2016, 2017:	Function: lecture preparation and substitution UWW 271 Contemporary analysis for ecology, lectures Responsible: Prof. Dr. Pascal A. Niklaus Location: University of Zurich